THE ROLE OF EPIPHYTIC BRYOPHYTES IN THE NET ACCUMULATION AND CYCLING OF NITROGEN IN A TROPICAL MONTANE CLOUD FOREST

By

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Abstract of Dissertation Presented to the Graduate School
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THE ROLE OF EPIPHYTIC BRYOPHYTES IN THE NET ACCUMULATION AND CYCLING OF NITROGEN IN A TROPICAL MONTANE CLOUD FOREST

By

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The functioning of epiphytic bryophytes in the net accumulation and cycling of nitrogen (N) in a tropical montane cloud forest was investigated at Monteverde, Costa Rica. Growth and net uptake of N by epiphytic bryophytes and decomposition and N dynamics of bryophyte litter were monitored to evaluate net N accumulation. Their role in N cycling was evaluated by estimating their effects on N inputs in wet deposition using a model that simulated net N retention by representative canopy components and by monitoring rates of net N mineralization from litter.

Annual growth of epiphytic bryophytes was 30% to 49% of initial sample mass, net production was estimated at 45 to 75 $g \cdot m^{-2} \cdot yr^{-1}$, and N accumulation was estimated at 0.7 to 1.1 $g\ N \cdot m^{-2} \cdot yr^{-1}$. Cumulative percent mass loss from litterbags was 17% after one year and 19% after two years in the canopy and 29% after one year on the forest floor. Nitrogen dynamics in litter in the canopy indicated that

±40% of the initial N content was released rapidly, but that the remaining N was recalcitrant. Net accumulation of N by epiphytic bryophytes was then estimated at 0.1 to 0.4 g N $m^{-2} \cdot yr^{-1}$ in the canopy and at 0.3 g $N \cdot m^{-2} \cdot yr^{-1}$ on the forest floor.

Epiphytic bryophytes and complex epiphyte assemblages retained from 60% to 98% of the N additions in artificial cloud water and N-enriched precipitation solutions in the laboratory. When a range of cloud water and precipitation events was simulated, model predictions suggested that epiphytic components retained from 33% to 75% of the N in wet deposition to the canopy. Annual net retention of N by epiphytic components was estimated at 0.4 g $N \cdot m^{-2} \cdot yr^{-1}$ and represented ±60% of inorganic N deposition to the canopy, thus they played a major role in regulating N fluxes in throughfall. Rates of net N mineralization from litter were greater than those characterizing canopy humus and mineralized N was potentially cycled rapidly to young bryophyte shoots and vascular epiphytes in the canopy. The functioning of epiphytic bryophytes at Monteverde is similar to that of terrestrial bryophytes in ecosystems where they are abundant.

CHAPTER 1
INTRODUCTION

Epiphytes in Tropical Montane Cloud Forests

Epiphytes are a conspicuous feature of the canopy in tropical montane cloud forests (TMCF). Epiphytic bryophytes (mosses and hepatics), lichens, vascular epiphytes, hemi-epiphytes, and their accumulated dead organic matter (DOM) form a nearly continuous cover on twigs, branches and stems of host trees and shrubs. Ecosystem level investigations in TMCF have indicated that epiphytes and DOM represent relatively large pools of carbon (C) and nitrogen (N), and contribute substantially to C and N fluxes in litterfall, throughfall, and stemflow to the forest floor (Nadkarni 1984, Coxson 1991, Nadkarni and Matelson 1992a,b, Coxson et al. 1992). Although high species diversity characterizes the epiphyte community (Madison 1977, Kress 1986, Gentry and Dodson 1987, Ingram and Nadkarni 1993), live epiphytic bryophytes and DOM together typically dominate in terms of mass (Table 1-1). Estimates of the N mass in epiphytes range from 2.5 to 44 g N m^{-2} ground area, equivalent to up to seven times the N mass in tree foliage (Tanner 1980a, Grubb and Edwards 1982, Nadkarni 1984, Hofstede et al. 1993). Estimates of N mass in live epiphytic bryophytes

Table 1-1. Mass of epiphytes, live epiphytic bryophytes, dead organic matter (DOM), live lichens, and live vascular epiphytes in tropical montane forests (g m^{-2} ground area).

Total for Epiphytes	Bryophytes	DOM	Lichens	Vascular Epiphytes	Reference
	Mass (g m^{-2} ground area)				
149	-	-	-	-	Golley et al. 1971[a]
263	-	-	-	150[α]	Tanner 1980b[b]
473	164	213	-	96	Nadkarni 1984[c]
520	85[ß]	180	-	255	Edwards and Grubb 1977[d]
1200	777[σ]	-	150	273	Veneklaas 1990[e]
1365	1030	245	-	90	Pócs 1982[f]
2000	1200	800	-	-	Coxson et al. 1992[g]
3320	150	2300	-	870[δ]	Nadkarni et al. unpub. data[h]
4400	685	2770	75	875	Hofstede et al. 1993[i]

a. No elevation reported, Darién, Panama
b. 1550 m, Mor Ridge site, Jamaica
c. 1580 m, Elfin forest site, Monteverde, Costa Rica
d. 3670 m, Mt. Kerigomna, New Guinea
e. 3370 m, Santa Rosa de Cabal, Colombia
f. 2120 m, Mt. Uluguru, Tanzania
g. 1330 m, La Soufrière, Guadaloupe
h. 1580 m, Leeward cloud forest site, Monteverde, Costa Rica
i. 3700 m, Santa Rosa de Cabal, Colombia
α. Bromeliads only
ß. Bryophytes and lichens not separated
σ. Bryophytes and accumulated DOM
δ. Epiphyte and host tree roots not separated

range from 0.9 to 15 g N m^{-2}; DOM typically represents the largest pool of N in the canopy of mature TMCFs.

In the few TMCFs where the contribution of epiphytes to litterfall has been monitored, epiphytes accounted for up to 8% (50 g m^{-2} yr^{-1}) of the mass and 7% (0.8 g N m^{-2} yr^{-1}) of the N fluxes in fine litterfall (Tanner 1980b, Veneklaas 1990, Nadkarni and Matelson 1992a). Across this range, epiphytic bryophytes composed up to 70% (35 g m^{-2} yr^{-1}) of the mass and 70% (0.5 g N m^{-2} yr^{-1}) of the N fluxes in epiphytic litterfall. Epiphytic bryophytes and DOM may also alter the fluxes of soluble organic C and N compounds to the forest floor. Coxson et al. (1992) and Coxson (1991) reported that the leaching of soluble C (primarily sugars and polyols) and soluble organic N was substantial when initially dry assemblages of epiphytic bryophyte and DOM in the upper canopy were rehydrated at a TMCF site in Guadeloupe. Total net fluxes were estimated at 12 g C m^{-2} yr^{-1} and 1.2 g N m^{-2} yr^{-1}, although some C and N containing compounds may have been reabsorbed by epiphytes and host tree foliage in the lower canopy.

Although there is considerable information concerning the physiology and mineral nutrition of both nonvascular and vascular epiphytes (Smith 1982, Benzing 1990, Bates and Farmer 1992), processes by which epiphytic bryophytes accumulate N and their functioning in the N cycle of these ecosystems are poorly characterized (Nadkarni 1984, Coxson 1991, Lugo and Scatena 1992). However, epiphytic bryophytes may contribute substantially to the productivity and nutrient cycles of TMCF because they (i) display a large amount of leaf area throughout the canopy, (ii) have moderate rates of net C fixation at the conditions that characterize many TMCF (Frahm 1987, 1990b, K. Clark unpub. data), leading to biomass production and net uptake of nutrients, (iii) may have relatively low rates of litter decomposition, (iv) retain and assimilate nutrients from a variety of sources, potentially altering nutrient fluxes to the forest floor (Grubb et al. 1969, Clark 1985, Nadkarni 1986a, Benzing 1990, Nadkarni and Matelson 1991), and (v) support both free living and symbiotic N_2-fixing cyanobacteria (Forman 1975, Pike 1978, Bentley and Carpenter 1984, Bentley 1987, D. Schaefer unpub. manuscript).

Net Accumulation of Nitrogen by Epiphytic Bryophytes

One of the hypothesized mechanisms leading to the net accumulation of N by epiphytic bryophytes is N accumulation in new growth. Although instantaneous photosynthetic and respiratory rates of epiphytic bryophytes have been relatively well documented (Hosokawa et al. 1964, Tobiessen et al. 1977, Frahm 1987, 1990b), estimates of growth and net primary production (NPP) of epiphytic bryophytes in TMCF are lacking. Because tissue N concentrations of epiphytic bryophytes range between 7 and 16 mg (g dry wt)$^{-1}$ (Grubb and Edwards 1982, Nadkarni 1984, Veneklaas 1990, Hofstede et al. 1993), net production drives the uptake of N from a variety of potential sources in the canopy, including atmospheric deposition and mineralization of N from DOM. Therefore, where their biomass and rates of NPP are relatively large, epiphytic bryophytes could be important in the accumulation of N in these ecosystems.

A second hypothesized mechanism leading to the net accumulation of N by epiphytic bryophytes is a relatively low rate of litter decomposition. Rates of vascular plant litter decomposition are reportedly low in TMCF when compared to tropical forests at lower elevations, leading to large accumulations of humus and soil organic matter on the forest floor (Jenny et al. 1949, Grubb 1977, Edwards and Grubb 1977, Nadkarni and Matelson 1992b). Decomposition of litter derived from epiphytic bryophytes may be particularly slow as a result of their accumulation of polyphenolic and aliphatic compounds, similar to those found in litter derived from terrestrial bryophytes (Berg 1984, Kälviäninen et al. 1985, Van Toreen 1988, Rochefort et al. 1990). As a consequence, epiphytic bryophytes may contribute disproportionately to N pools in DOM in the canopy and on the forest floor of these ecosystems.

In temperate ecosystems where they are abundant, terrestrial bryophytes have been shown to be important in the net accumulation of N, because rates of N uptake in new growth typically exceed rates of litter decomposition and N loss (Oechel and Van Cleve 1986, Malmer 1988, Urban and Eisenreich 1988, Malmer and Wallen 1993). Epiphytic bryophytes may be similarly important in the net accumulation of N in TMCF.

Role of Epiphytic Bryophytes in Nitrogen Cycling

One of the hypothesized sources of N for epiphytic bryophytes is inorganic N in atmospheric deposition. Although atmospheric deposition has both wet and dry components, wet deposition is likely the dominant form of atmospheric input to TMCF (Vogelmann 1973, Cavelier and Goldstein 1989, McDowell and Asbury 1993). Epiphytic bryophytes may have a considerable ability to retain and assimilate nitrate (NO_3^-) and ammonium (NH_4^+) from wet deposition and canopy solutions because (i) they store relatively large volumes of solution adjacent to metabolically active tissue (Pócs 1982, Veneklaas et al. 1990), and (ii) they may have a relatively low diffusional resistance to ion uptake due to minimal cuticular development (Richardson 1981, Proctor 1984, Schaefer and Reiners 1990). Sphagnum and other terrestrial bryophytes, which are physiologically similar to epiphytic bryophytes, have also been shown to retain and assimilate inorganic N from relatively dilute solutions and wet deposition (Weber and Van Cleve 1984, Woodin and Lee 1987, Urban et al. 1988, Van Toreen et al. 1990, Bowden 1991).

In contrast to nonvascular epiphytic components, vascular plant foliage characterizing TMCF may retain and assimilate relatively little inorganic N from atmospheric deposition. It is hypothesized that the relatively thick, waxy cuticle on foliar surfaces results in rapid solution runoff and a relatively large diffusional resistance to the uptake of inorganic N (Lovett et al. 1989, Garten and Hanson 1990, Schaefer and Reiners 1990, Wilson 1992, Lumme 1994).

Epiphytes function to increase the interception of cloud water and precipitation because their surface area contributes to the aerodynamic roughness of the canopy (Lovett 1984, Nadkarni 1984, 1986a, Lovett and Reiners 1986). Retention and assimilation of inorganic N by epiphytic bryophytes and DOM from canopy solutions potentially alter inorganic N fluxes in throughfall and stemflow (Clark and Nadkarni 1990, 1992, McDowell and Asbury 1993). Where they are abundant in the canopy, therefore, epiphytic bryophytes and DOM may play a major role in regulating inorganic N fluxes from the atmosphere to the forest floor.

A second hypothesized mechanism by which epiphytic bryophytes potentially affect rates of N cycling in TMCF is via the leaching and net mineralization of N from bryophyte-derived litter. In contrast to the hypothesized low rates of mass loss, recently formed bryophyte litter may also be characterized by initially high rates of N leaching and net N mineralization. This apparently contradictory behavior is presumably due to the rapid release of labile C and N pools, minimal immobilization in microbial biomass, and then a relatively slow release of the remaining N in litter

(Clymo and Hayward 1982, Brock and Bregman 1989, Verhoeven et al. 1990). Consequently, rates of N cycling within bryophyte shoots may be substantial (Malmer 1988, Urban and Eisenreich 1988, Bates 1992). Nitrogen release from litter potentially regulates N availability in the canopy because fine roots of vascular epiphytes and host trees are associated with bryophyte-derived DOM (Nadkarni 1981, ter Steege and Cornelissen 1989, Vance and Nadkarni 1992, Ingram and Nadkarni 1993). Although microbial activity in canopy humus (as measured by CO_2 evolution in the laboratory) was comparable to that from forest floor humus, net mineralization rates of N were low and lower than those reported from the upper soil horizons at a number of TMCF sites (Vance and Nadkarni 1990, Marrs et al. 1988, Vitousek et al. 1988), suggesting that net N release from more highly decomposed DOM in the canopy was limited. However, no field studies have evaluated the importance of litter derived from epiphytic bryophytes in N cycling and N supply in the canopy of TMCF.

Epiphytic Bryophytes and Increased Nitrogen Deposition

Understanding the functional significance of epiphytic bryophytes and DOM in the net accumulation and cycling of N in TMCF is a prerequisite to evaluating the effects of increased N deposition to these ecosystems. Seasonal biomass burning, conversion of forest to pasture and croplands, and other land use changes have increased N emissions in tropical regions (Crutzen and Andreae 1990, Keller et al. 1991, Galloway et al. 1994), leading to higher concentrations of inorganic N in cloud water and precipitation (Lewis 1981, Kelman et al. 1982, Clark et al. 1993). Epiphytic bryophytes and other canopy biota may be sensitive to the effects of increased N deposition (Press et al. 1986, Lee et al. 1990, Marrs 1993, Jauhiainen et al. 1994); therefore, it is imperative to understand their roles in the net accumulation and cycling of N in the canopy. This is an important first step in estimating realistic "critical loads" of N for these ecosystems (*sensu* Schulze et al. 1989, Aber 1992, Stevens et al. 1994) and predicting long-term effects of increased N deposition to diverse epiphyte communities and TMCF ecosystems as a whole.

Objectives and Research Questions Addressed

The objectives of this research were to determine the functional roles of epiphytic bryophytes and DOM in the net accumulation and cycling of N in a TMCF. Specific research questions that addressed the net accumulation of N by epiphytic bryophytes and their accumulated DOM were:

1. What are the rates of net primary production (NPP) and N accumulation by epiphytic bryophytes (Chapter 3)?
2. What are the rates of mass loss from epiphytic bryophyte litter in the canopy and on the forest floor and how do they compare to the rates of mass loss from fine vascular plant litter at these locations (Chapter 6)?

3. What is the rate of N loss from epiphytic bryophyte litter in the canopy (Chapter 6)?

Specific research questions that addressed N cycling by epiphytic bryophytes and their accumulated DOM were:

4. What are the effects of epiphytic bryophytes and assemblages of bryophytes, vascular epiphytes, and DOM on inorganic N additions in cloud water and precipitation solutions (Chapter 4)?
5. What are the effects of vascular plant foliage in the TMCF canopy on inorganic N additions in cloud water and precipitation solutions (Chapter 4)?
6. To what extent do epiphytic bryophytes and assemblages of bryophytes, vascular epiphytes, and DOM alter inorganic N fluxes in wet deposition as solutions pass through the canopy to the forest floor (Chapter 5)?
7. What are the rates of net mineralization of inorganic N from epiphytic bryophyte litter and how do they compare to those characterizing more highly decomposed humus in the canopy (Chapter 6)?.

The experiments designed to address these questions are detailed in the following five chapters. The results of experiments that addressed questions four and five were synthesized using a model to simulate canopy hydrology and the effects of representative canopy components on inorganic N fluxes in throughfall to address question six.

Net accumulation of N by epiphytic bryophytes, implications of the results, and overall conclusions are discussed in Chapter 7.

CHAPTER 2
SITE DESCRIPTION

Investigations were conducted in a 4 ha plot of primary forest in the research area of the Monteverde Cloud Forest Reserve (MVCFR) in the Cordillera de Tilarán, west-central Costa Rica (10°18'N, 84°48'W). Slopes and ridges in the MVCFR are similar to other tradewind-dominated mid-elevation montane forests in terms of climate, forest physiognomy and epiphyte mass and diversity (Lawton and Dryer 1980, Weaver et al. 1986, Städtmuller 1987, Bruijnzeel and Proctor 1993).

Three distinct seasons are differentiated primarily by the seasonal migration of the intertropical convergence zone: (i) the dry season (February to April), characterized by moderate northeasterly tradewinds and advective cloud and mist, (ii) the wet season (May to October), characterized by convective precipitation, and (iii) the transition season (November to January), characterized by strong tradewinds and advective mist and precipitation. Measured annual cloud water and precipitation depth at the site was 407 cm during 1991-92, 60% of which fell during the wet season. Long-term (1959 to 1993) mean annual precipitation depth measured at a site ca. 3 km NW and 100 m downslope from the study site is 250 cm, but advective cloud water and precipitation deposition was underestimated (J. Campbell, pers. comm.). Mean monthly minimum and maximum temperatures during 1991-92 ranged between 13.9 and 16.5 °C and between 17.6 and 21.1 °C, respectively.

The study site is located ca. 1.5 km southwest of MVCFR Headquarters. Elevation of the site ranges between 1480 and 1520 m. The site is in the tropical lower montane wet forest zone of Holdridge (1967), further classified by Lawton and Dryer (1980) as leeward cloud forest. The soil is classified as a typic dystrandept (Vance and Nadkarni 1990, USDA 1992). The H and A_1 horizons (ca. 0-20 cm depth) are highly organic and the A_2 and B horizons (ca. 20-180 cm depth) poorly differentiated (Vance and Nadkarni 1990, 1992). Forest floor mass is estimated at ca. 1050 g m^{-2} (Nadkarni and Matelson 1992b). Canopy height is 15-32 m with a few emergents to 35 m, and stem density is ca. 160 stems ha^{-1} (>30 cm DBH). Canopy species are primarily broad-leaved evergreens. The five most frequently occurring plant families in the canopy are the Lauraceae, Moraceae, Leguminoseae, Sabiaceae, and Meliaceceae.

Total epiphyte mass is estimated at 3300 g m^{-2} ground area (Nadkarni et al. 1993). Small twigs in the upper and outer portions of the canopy have a substantial coverage of pendant, fan and tail-forming bryophytes (life-form terminology sensu Mägdefrau 1982, During 1992). Fan, tail, weft and mat-forming bryophytes are abundant on large twigs and small branches. These life-forms, along with turf and cushion-forming bryophytes, frequently occur on large branches and main stems. Litter and humus accumulations occur beneath most bryophyte life-forms (Vance and Nadkarni 1992, Ingram and Nadkarni 1993).

The diverse vascular epiphyte community has been described by Lawton and Dryer (1980), Nadkarni (1986b) and Ingram and Nadkarni (1993). Major groups represented include the Araceae, Orchidaceae, Ericaceae, Bromeliaceae, and members of the Filicales. Vascular epiphytes are frequently associated with bryophytes and DOM on small branches, large branches and main stems. Larger branch surfaces and branch junctions with main stems are typically covered with thick epiphyte mats composed of bryophytes, herbaceous and woody epiphytes and considerable accumulations of DOM (Vance and Nadkarni 1990, 1992, Ingram and Nadkarni 1993). Hemiepiphytes in the Araliaceae, Clusiaceae, Melastomataceae, and Moraceae are also present.

CHAPTER 3
RATES OF GROWTH, NET PRODUCTION, AND NET NITROGEN UPTAKE BY EPIPHYTIC BRYOPHYTES

Introduction

Epiphytic bryophytes may play important functional roles in the production of biomass and the accumulation of nitrogen (N) and other nutrients in TMCF. Net carbon gain by epiphytic bryophytes is controlled by interactions among light levels, temperature, plant water status, and nutrient availability (Proctor 1982, 1990, Frahm 1987, 1990a). While epiphytic bryophytes have relatively low photosynthetic capacities when compared to C_3 vascular plants, they also are characterized by low light compensation points and low to moderate rates of respiration at the ambient temperatures typical of TMCF (Hosokawa et al. 1964, Tobiessen et al. 1978, Frahm 1990b, K. Clark unpub. data). Frequent cloud immersion and precipitation, and low vapor pressure deficit of the atmosphere reduce periods of low water availability in TMCF, considered to be a major constraint on net C gain by poikilohydric bryophytes (Hosokawa et al. 1964, Proctor 1982, 1990). Therefore, environmental conditions characterizing TMCF may generally favor the growth and net primary production (NPP) of epiphytic bryophytes (Richards 1984, Frahm 1987, 1990a,b).

Biomass production by epiphytic bryophytes drives the uptake of N and other nutrients from a variety of potential sources, including atmospheric deposition and mineralization from dead organic matter (DOM) in the canopy (Grubb et al. 1969, Clark 1985, Nadkarni 1986a, Benzing 1990, Vance and Nadkarni 1990, Nadkarni and Matelson 1991). Tissue N concentrations range from 7 to 16 mg N (g dry wt)$^{-1}$ (Nadkarni 1984, Veneklaas 1990, Hofstede et al. 1993); thus, where their biomass and rates of NPP are relatively large, epiphytic bryophytes may be important in the accumulation of N in these ecosystems. Where NPP of epiphytic bryophytes exceeds the rate of litterfall to the forest floor, epiphytic bryophytes may also be important in the accumulation of mass and N in the canopy.

The objectives of this study were (i) to monitor the growth of epiphytic bryophytes and estimate their annual NPP, (ii) to analyze tissue N concentrations in new growth and estimate N accumulation by epiphytic bryophytes, and (iii) to estimate the accumulation of biomass and N by epiphytic bryophytes in the canopy of a TMCF.

Materials and Methods

Mass Accumulation

Mass accumulation by samples of epiphytic bryophytes was estimated using mesh tube or cup enclosures in the canopy (Russel 1988). Epiphytic bryophyte samples were collected from the canopy and from recent treefalls

(<2 weeks old) at the field site and immediately transported to the laboratory. Samples were pooled into three groups: (i) pendant bryophytes, (ii) fan- and tail-forming bryophytes, and (iii) mat-, weft-, and turf-forming bryophytes (life-form terminology sensu Mägdefrau 1982, During 1992). These groupings were consistent with their co-occurrence on twigs and smaller branches, and larger branches and trunks, respectively. Litter and brown shoots were removed so that samples consisted of primarily live, green shoots.

Pendant bryophytes

Samples of pendant bryophytes were separated into sets consisting of two subsamples. Within sets, one subsample (2 to 5 g fresh weight) was weighed and then loosely packed into an open nylon mesh tube (1 cm mesh size, 20 cm long, 8 to 10 cm in diameter, with an open top and a 0.2 cm mesh size base). The other subsample was weighed immediately, dried at 60 °C for 48 hours, and weighed again to calculate the initial water content and hence the dry mass of the subsample in the mesh tube.

Fan- and tail-forming bryophytes

Samples of fan- and tail-forming bryophytes were also separated into sets consisting of two subsamples. One subsample was weighed and then loosely packed into an open nylon mesh tube (1 cm mesh size, 10-12 cm long, 7-8 cm in diameter, with an open top and a 0.2 cm mesh size base). The other subsample was weighed, dried and weighed again to calculate the initial dry mass of the subsample in the mesh tube.

Twelve trees (> 50 cm DBH) at the study site were selected, representing the most frequently occurring genera in the canopy (Table 3-1). Nylon lines were placed over small branches in the upper canopy using a modified slingshot connected to a fishing reel. Mesh tubes containing samples were tied to these lines; pendant bryophyte samples were placed above fan- and tail-forming bryophyte samples. Mesh tubes were positioned as close as possible to twigs and branches in the middle to upper canopy. Three to six mesh tubes were placed within each tree canopy. Samples were collected at the end of four six-month periods: June to December 1990, January to June 1991, August 1991 to March 1992, and April to September 1992. After retrieval, shoots emerging from the mesh tubes were removed with scissors, then the remaining shoots confined in the mesh tubes were removed. All shoots were subsequently dried at 60 °C for 48 hours and weighed.

Mat-, weft-, and turf-forming bryophytes

Samples of mat-, weft-, and turf-forming bryophytes were separated into sets consisting of two subsamples. Within sets, one subsample (5 to 10 g fresh weight) was weighed and placed in a polypropylene cup (7.5 cm diameter, 5 cm tall, with an open top and a 0.2 cm mesh size base to facilitate drainage). The other subsample was weighed immediately, dried at 60 °C for 48 hours, and weighed again

Table 3-1. Trees used for monitoring mass accumulation by epiphytic bryophytes: (i) number of trees in which mesh tubes containing pendant and fan- and tail-forming bryophytes or cups containing mat-, weft-, and turf-forming bryophytes were placed, (ii) number of mesh tubes placed in each tree species, and (iii) number of cups placed in each tree species.

Species	n	Number of Mesh Tubes	Number of Cups
Ocotea tonduzii	5, 2	50	8
Meliosma ideopoda	2, 1	21	8
Ficus tuerckheimii	2, 1	17	5
Pouteria viride	1, 0	13	4
Inga tonduzii	1, 0	11	0
Unknown sp.	1, 0	3	0
Total	12, 5	115	25

to calculate the initial water content and dry mass of the subsample in the cup.

Five trees at the study site were selected (Table 3-1). Mid-canopy locations were accessed using modified rock climbing techniques. Ten accessible locations along medium and large branches were selected, and two to five of these were chosen randomly in each tree for sample placement. Samples were collected after two six-month periods: August 1991 to March 1992 and April to September 1992. Samples were removed from the cups, dried at 60 °C for 48 hours and weighed.

Tissue Nitrogen Concentrations

Tissue N analyses were performed on samples of epiphytic bryophytes collected from the canopy of five trees because there was insufficient sample mass to analyze new growth from the mesh tubes and cups. Dead organic matter was removed from samples, and samples were pooled into the same three life-form groups as above. New shoots were separated from samples of each life-form group with scissors. Tissue N concentrations of whole shoots from the life-form groups were also analyzed. Samples were dried at 60 °C for 48 hours and stored in clean polypropylene vials until they were analyzed (Appendix A).

Data Analyses

Emergent shoot mass (initial value = 0), mass accumulation or loss in mesh tubes, and the sum of shoot emergence and mass accumulation or loss in mesh tubes were calculated as a percent change from estimated initial dry mass for samples of pendant bryophytes and fan- and tail-forming bryophytes in mesh tubes. Data from both life-form groups in the mesh tubes were pooled together for the analyses here. Mass accumulation or loss by mat-, weft-, and turf-forming bryophytes in cups was calculated as a percent change of initial dry mass in the cups. Two estimates of mean mass accumulation by epiphytic bryophyte samples were calculated from these data. Lower values for mean mass accumulation were calculated by comparing the sum of shoot emergence and mass accumulation in mesh tubes or mass accumulation in cups to the rate of mass loss from epiphytic bryophyte litterbags in the canopy over an initial six month period (Chapter 6); values that exceeded 14.3% mass loss were removed from the data sets. Higher values for mean mass accumulation were calculated by further removing all negative values of the sum of shoot emergence and mass accumulation in mesh tubes or mass accumulation in cups from the data sets.

For pendants and fan- and tail-forming bryophytes, one-way ANOVAs were used to detect differences in (i) emergent shoot mass, (ii) mass accumulation in mesh tubes, and (iii) mean mass accumulation estimates as a function of sampling period. One-way ANOVAs were also used to detect differences in mean mass accumulation estimates among life-form groups over all sampling periods. For mat-, weft-, and turf-forming bryophytes, T-tests were used to detect differences in mean mass accumulation estimates among the two sampling periods. T-tests were also used to detect differences in tissue N concentrations among life-form groups.

Annual percentage growth of epiphytic bryophytes was calculated by multiplying mean mass accumulation estimates for the six month sampling periods by two. Net production was estimated by multiplying annual percent growth rates by an estimate of epiphytic bryophyte biomass at the site (150 g m^{-2}; Nadkarni et al. 1993). Accumulation of N by epiphytic bryophytes was estimated by multiplying the two NPP estimates by the mean tissue N concentration in new growth, assuming that there were no seasonal changes in N concentrations of new shoots. Mass and N accumulation by epiphytic bryophytes in the canopy were calculated by subtracting an estimate of epiphytic bryophyte litterfall fluxes to the forest floor (35 g m^{-2} yr^{-1} and 0.5 g N m^{-2} yr^{-1}; Nadkarni and Matelson 1992a) from NPP and N accumulation estimates. T-tests were used to detect mass and N accumulation by epiphytic bryophytes in the canopy. Normality of all data sets was established, and homogeneity of group variances was confirmed with Bartlett's test. SYSTAT statistical packages (Wilkinson 1987) were used for all analyses.

Results

Mass Accumulation

Mass of emergent shoots of pendants and fan- and tail-forming bryophytes in mesh tubes was different among sampling periods (ANOVA, $F_{2,68}=6.853$, $P < 0.01$), but differences in mass accumulation in mesh tubes and in the estimates of mean mass accumulation were not detected among these periods (Table 3-2). Mean mass accumulation estimates for mat-, weft-, and turf-forming bryophytes in cups were not different among the two sampling periods (Table 3-3).

Differences in the mean mass accumulation estimates among the two life-form groups were not detected. Therefore, estimates for both life-form groups were pooled, and resultant values were 15.5% ± 2.4% and 24.9 ± 2.7% (mean % ± 1 s.e.), respectively. Annual growth rates of epiphytic bryophytes calculated as a percent of initial mass from the lower and higher mean mass accumulation estimates were 30.0% ± 4.8% yr^{-1} and 49.9% ± 5.4% yr^{-1} (mean % ± 1 s.e.), respectively (Table 3-4).

Net Production

Annual NPP of epiphytic bryophytes estimated as the product of epiphytic bryophyte biomass at the site and (i) the lower annual growth rate estimate or (ii) the higher annual growth rate was 46 ± 7 and 74 ± 8 g m^{-2} yr^{-1} (mean ± 1 s.e.), respectively.

Table 3-2. Mean mass accumulation (as % change of initial mass over six months ± 1 s.e.) by pendant and fan- and tail-forming epiphytic bryophytes in mesh tubes.

Time Period	Percent Change in Mass (mean % ± 1 s.e.)			
	a. Emergent Shoots	b. Shoots in Mesh Tubes	c. Samples ≤ 14.3% Mass Loss	d. Samples ≤ 0.0% Mass Loss
June-Dec 1990	13.6 ± 2.5^{a} (10)	-0.7 ± 5.6 (10)	12.9 ± 7.7 (10)	32.7 ± 8.1 (5)
Jan-June 1991	n.d.	n.d.	14.6 ± 3.6 (14)	19.7 ± 2.9 (11)
Aug-Mar 1992	6.8 ± 1.0^{b} (32)	19.0 ± 4.9 (32)	22.4 ± 5.0 (32)	28.4 ± 5.2 (27)
Apr-Sept 1992	4.7 ± 1.3^{b} (28)	11.0 ± 4.4 (28)	15.7 ± 5.3 (28)	27.1 ± 6.3 (19)
Mean of Sampling Periods$^{\alpha}$	--	12.9 ± 3.0 (70)	17.7 ± 2.8 (84)	26.8 ± 3.1 (62)

a. shoots emerging from mesh tubes, b. shoots confined in mesh tubes, c. sum of a. and b. where samples ≤ 14.3% mass loss, and d. sum of a. and b. where samples ≤ 0.0% mass loss.
Sample size is in parentheses.
Superscripts indicate significant differences among time periods (ANOVA, $F_{2,68}=6.853$, $p < 0.01$)
n.d. = not determined.
α. Where differences among sampling dates were not significant.

Table 3-3. Mean mass accumulation (as % change of initial mass over six months ± 1 s.e.) by mat-, weft- and turf-forming epiphytic bryophytes in cups.

Time Period	Percent Change in Mass (mean % ± 1 s.e.)	
	Samples ≤ 14.3% Mass Loss	Samples ≤ 0.0% Mass Loss
Aug-Mar 1992	7.6 ± 5.2 (14)	16.6 ± 6.2 (9)
Apr-Sept 1992	1.1 ± 4.8 (9)	14.9 ± 4.5 (4)
Mean of Sampling Periods	5.0 ± 3.7 (23)	16.1 ± 4.4 (13)

Sample size is in parentheses.

Table 3-4. Mean annual percent growth (as a percent change of initial mass ± 1 s.e.) calculated for pendant, fan- and tail-forming bryophytes in mesh tubes and mat-, weft- and turf-forming bryophytes in cups (from Tables 3-2 and 3-3).

Bryophyte Life-form Group	Annual Percent Growth (mean % ± 1 s.e.)	
	Samples ≤ 14.3% Mass Loss	Samples ≤ 0.0% Mass Loss
Pendants + Fans + Tails	35.4 ± 5.6 (84)	53.6 ± 6.2 (62)
Mats + Wefts + Turfs	10.0 ± 7.4 (23)	32.2 ± 8.8 (13)
Mean of Life-form Groups	30.0 ± 4.8 (107)	49.9 ± 5.4 (75)

Sample size is in parentheses.

Tissue Nitrogen Concentrations

Mean tissue N concentrations in new shoots of the two life-form groups were similar (Table 3-5). Mean tissue N concentrations in mature shoots of pendants, fans and tails were lower than those in mats, wefts and turfs (T-test, $P < 0.05$).

Nitrogen Accumulation

Estimates of nitrogen accumulation by epiphytic bryophytes calculated as the product of the two NPP estimates and new shoot N concentrations were 0.7 ± 0.1 and 1.1 ± 0.1 g N m^{-2} yr^{-1} (mean ± 1 s.e.), respectively.

Accumulation of Mass and Nitrogen in the Canopy

Estimates of mass accumulation by epiphytic bryophytes in the canopy calculated by subtracting epiphytic bryophyte litterfall flux to the forest floor from the two NPP estimates were 11 ± 7 and 39 ± 8 g m^{-2} yr^{-1} (mean ± 1 s.e.), respectively. Estimates of N accumulation by epiphytic bryophytes in the canopy calculated in a similar manner were 0.2 ± 0.1 and 0.6 ± 0.1 g N m^{-2} yr^{-1}. Neither the NPP estimates nor the estimates of net uptake of N were different from mass or N fluxes in epiphytic bryophyte litterfall to the forest floor, due in part to high variability in the NPP and net N uptake estimates.

Table 3-5. Nitrogen concentrations (mean mg N (g dry wt)$^{-1}$ ± 1 s.e.) in new shoots and mature shoots of pendant, fan- and tail-forming bryophytes and mat-, weft- and turf-forming bryophytes.

Bryophyte Life-form Group	Nitrogen Concentration (mean mg N (g dry wt)$^{-1}$ ± 1 s.e.)	
	New Shoots	Mature Shoots
Pendants and Fans + Tails	14.4 ± 1.6 (10)	13.7 ± 0.7^{a} (24)
Mats + Wefts + Turfs	16.0 ± 1.4 (10)	17.0 ± 0.4^{b} (16)
Mean of Life-Form Groups	15.3 ± 1.6 (20)	15.0 ± 0.5 (40)

Superscripts indicate significant differences among life-form groups (T-test, $P < 0.05$).
Sample size is in parentheses.

Discussion

Mass loss from epiphytic bryophyte samples in mesh tubes and cups could be due to three factors: (i) disturbance when samples were placed in or removed from the canopy, (ii) natural disturbances due to wind or arboreal animal activity, and (iii) leaching of leaves, stems, and particulates from mesh tubes and cups by precipitation. Mass loss due to herbivory was probably minimal (e.g., Richardson 1981, Gerson 1982, Longton 1992).

Annual percent growth rates of epiphytic bryophytes have been assessed in one other study. Jacobsen (1978) reported a mean annual growth rate of 8.2% for epiphytic bryophytes on the lowest 2 m of stems over a 3-year period in the Transvaal, which is considerably lower than estimates reported here. Annual percent growth rates calculated for epiphytic bryophytes at Monteverde are within the range of annual percent growth rates (17% to 70%) reported for terrestrial bryophytes in a number of ecosystems (Rieley et al. 1979, Binkley and Graham 1981, Oechel and Van Cleve 1986, Lindholm and Vasander 1990, Bowden 1991).

Net production estimates for epiphytic bryophytes are at the low end of NPP estimates for terrestrial bryophytes in a range of ecosystems where bryophytes are relatively abundant (Table 3-6). High NPP estimates for terrestrial bryophytes, particularly for Sphagnum and Polytrichum, are frequently a result of high cover values (80 to 135%) and large biomass values (2500 to 4500 g m^{-2}) rather than high

Table 3-6. Net primary production of bryophytes in selected ecosystems. Genus listed where indicated.

Genus	Production ($g\ m^{-2}\ yr^{-1}$)	Location	Reference
Epiphytic Bryophytes	46 to 74	Costa Rica	This study
Homalothecium	190	N Canada	Busby et al. 1978
Polytrichum	430 to 650	Antarctica	Collins 1976
	450 to 507	Antarctica	Longton 1970
	790	W Virginia	Wieder and Lang 1983
	1000	New Hampshire	Bowden 1991
Various Spp.	21 to 754	Sub-antarctic	Russel 1985
	40	Oregon	Binkley and Graham 1981
	72 to 126	Alaska	Oechel and Van Cleve 1986
	170 to 210	NW Wales	Reiley et al. 1978
Sphagnum	25 to 125	S Sweden	Wallen et al. 1988
	35 to 213	England	Forrest and Smith 1975
	50 to 350	England	Clymo and Reddaway 1971
	52 to 303	NW Ontario	Rochefort et al. 1990
	90	S Sweden	Damman 1978
	150 to 490	S Finland	Lindholm and Vasander 1990
	195 to 288	S Finland	Pakarinen 1978
	240	NE Ontario	Pakarinen and Gorham 1983
	320 to 380	Minnesota	Grigal 1985
	450 to 610	W Virginia	Wieder and Lang 1983

rates of growth (Russel 1985, 1990, Bowden 1991, Malmer and Wallen 1993). Unfortunately, biomass values are rarely reported with NPP estimates, making direct comparisons difficult. It is also possible that NPP estimates for epiphytic bryophytes at Monteverde are low due to uncertainties in the biomass estimate, which appears to be low when compared to other TMCF sites characterized by a large epiphyte mass (Table 1-1).

Tissue N concentrations of epiphytic bryophytes at Monteverde were greater than those reported for epiphytic bryophytes at other sites (Table 3-7). Tissue N concentrations were also greater than those of most terrestrial bryophytes with the exception of Sphagnum from regions with high rates of N deposition from the atmosphere (Ferguson et al. 1984, Malmer 1988, Aerts et al. 1992).

Although NPP of epiphytic bryophytes is relatively low due to low biomass in the canopy, estimated N accumulation is within the range of estimates reported for terrestrial bryophytes because of the relatively high tissue N concentrations of epiphytic bryophytes at Monteverde (Table 3-8).

Annual NPP of epiphytic bryophytes represented 6% to 9% of annual foliage production at this site (ca. 800 g m^{-2} yr^{-1}; Nadkarni and Matelson 1992b). Accumulation of N by epiphytic bryophytes represented 4% to 7% of the estimated annual net uptake of N by foliage. In contrast to vascular plant foliage, however, a relatively large portion of the N

Table 3-7. Nitrogen concentrations (mg N (g dry wt)$^{-1}$) of mature shoots of: (i) epiphytic bryophytes in tropical montane cloud forests, (ii) terrestrial bryophytes other than Sphagnum, and (iii) Sphagnum (mean ± 1 s.e., where reported).

Location	N concentration (mg N (g dry wt)$^{-1}$)	Reference
Epiphytic Bryophytes		
Monteverde, Costa Rica	15.0 ± 0.5	This study
Santa Rosa de Cabal, Colombia	7.1	Hofstede et al. 1993
Santa Rosa de Cabal, Colombia	9.7 ± 0.4[a]	Veneklaas 1990
Marafunga, New Guinea	12.7	Grubb and Edwards 1982
Monteverde, Costa Rica	15.8 ± 0.8[a]	Nadkarni and Matelson 1992a
Monteverde, Costa Rica	16.4 ± 0.7	Nadkarni 1984
Terrestrial Bryophytes		
Atkasook, Alaska	5.0 ± 1.0 to 9.5 ± 2.0	Chapin et al. 1980
Marion Island, Antarctica	8.9 ± 1.3	Russel 1987
A. J. Andrews, Oregon	9.0 to 11.0	Binkley and Graham 1981
Luquillo Forest, Puerto Rico	9.1	Frangi and Lugo 1992
Wylrer Akkers, Netherlands	11.3[b]	Van Tooren et al. 1987

Table 3-7 continued.

Location	N concentration (mg N (g dry wt)$^{-1}$)	Reference
Sphagnum		
Andoya, Scandinavia	6.4 ± 1.0	Malmer 1988
Stordalen Mire, N. Sweden	7.0 ± 0.4	Aerts et al. 1992
Berwyn Mnts. N. Wales	7.0 ± 0.1 to 11.0 ± 0.1	Ferguson et al. 1984
Various, S. Finland	7.0 to 8.3	Pakarinen 1978
Tornetrask, Scandinavia	7.7 ± 0.7	Malmer 1988
Moor House, England	8.6 ± 0.3	Heal and Smith 1978
Various, SW Sweden	11.5 ± 1.4[b]	Malmer 1988
Akhult Mire, S. Sweden	13.5 ± 0.8[b]	Aerts et al. 1992
Holm Moss, S. Pennines	17.0 ± 0.1 to 20.0 ± 0.2[c]	Ferguson et al. 1984
Holm Moss, S. Pennines	to 33.5[b]	Ferguson et al. 1984

a. Epiphytic bryophytes in litterfall traps
b. Regions of high N deposition
c. Transplanted to sites of high N deposition

Table 3-8. Nitrogen contents in live bryophyte biomass, N accumulation in net primary production, and net ecosystem N accumulation in selected ecosystems where bryophytes are abundant (mean ± 1 s.e., where reported).

Ecosystem	N in Biomass ($g\ m^{-2}$)	N Accumulation ($g\ m^{-2}\ yr^{-1}$)	Net Ecosystem N Accumulation ($g\ m^{-2}\ yr^{-1}$)
Tropical Montane Cloud Forest[a]	2.3	0.7 ± 0.1 to 1.1 ± 0.1	n.d.
Pseudotsuga Forest[b]	0.9	0.4	n.d.
Polytrichum, Successional[c]	3.3 ± 0.4	1.2 ± 0.2	0.6[α], 1.0[ß]
Sub-arctic bog[d]	4.4	0.4	0.4[α], 0.9[ß]
Sphagnum bog[e]	5.4 ± 0.2	4.0 ± 0.2	0.7[α], 1.2[ß]
Alaska Taiga[f]	7.2	1.3	n.d.

a. This study
b. Binkley and Graham 1981
c. Bowden 1991
d. Rosswall and Granhall 1980
e. Urban and Eisenreich 1988
f. Oechel and Van Cleve 1986
α. N accumulation calculated from input-output budget,
ß. N accumulation calculated from peat accumulation.
n.d. = not determined.

requirement of epiphytic bryophytes may have been met by inorganic N inputs from the atmosphere (Chapters 4, 5). Therefore, epiphytic bryophytes are likely to be important in transforming "pulses" of N in atmospheric deposition to more recalcitrant forms of N in biomass. Although estimates of N leaching from the soil are lacking for this site, accumulation of N in bryophyte biomass and DOM presumably reduces overall losses. In this context, the functioning of epiphytic bryophytes in the accumulation of N in this ecosystem is similar to that of terrestrial bryophytes in a variety of other ecosystems where they are relatively abundant (Oechel and Van Cleve 1986, Urban and Eisenreich 1988, Longton 1992, Malmer and Wallen 1993)(Table 3-8).

Although estimates of NPP and N accumulation by epiphytic bryophytes were not significantly greater than the rate of litterfall to the forest floor, results suggested that they accumulated 11 to 39 g mass m^{-2} yr^{-1} and 0.2 to 0.6 g N m^{-2} yr^{-1} in the canopy. Therefore, when the basal portions of shoots die, they apparently contribute to C and N pools in DOM in the canopy (Chapter 6).

There is little information concerning the effects of N availability on NPP of epiphytic bryophytes in TMCF, but increased N deposition due to current land use practices and biomass burning in tropical regions (Crutzen and Andreae 1990, Keller et al. 1991) may affect the NPP and N status of epiphytic bryophytes in various ways. Increased N supply to terrestrial bryophytes has stimulated NPP in some cases

(Rochefort et al. 1990, Aerts et al. 1992), and caused declines in others (Press et al. 1986, Rudolf et al. 1987, Thompson and Baddeley 1991, Pitcairn et al. 1991, Jauhiainen et al. 1994). The direction and magnitude of these effects are apparently a function of deposition rates, although the effects of pollutants other than SO_2 have not been evaluated in field studies. However, long-term increased N deposition has apparently caused a substantial decline in NPP and biomass of Sphagnum and Racomitrium in some regions of Europe (Tallis 1964, Press et al. 1986, Baddeley et al. 1994).

Increased N deposition has also led to an increase in tissue N concentrations in both epiphytic and terrestrial bryophytes at temperate and boreal sites (Ferguson et al. 1984, Malmer 1988, Farmer et al. 1991, Aerts et al. 1992, Baddely et al. 1994). Where NPP is stimulated by increased N deposition, subsequent control over NPP may be exerted by limitations of other nutrients, particularly phosphorus (P) (Aerts et al. 1992). Although tissue N concentrations of epiphytic bryophytes at Monteverde were higher than those in epiphytic bryophytes from other TMCF sites, N to P ratios are currently within the range of ratios reported for bryophytes from sites characterized by low rates of N deposition from the atmosphere (Nadkarni 1984, Malmer 1988, Aerts et al. 1992, Hofstede et al. 1993).

Increased N deposition and N availability have also caused significant changes in competitive interactions and community composition in a range of ecosystems characterized by low nutrient status (Willis 1963, Verhoeven and Schmitz 1991, Bowman et al. 1993, Marrs 1993, Baddeley et al. 1994). Higher N concentrations in epiphytic bryophyte litter may accelerate rates of N leaching and decomposition (e.g., Clymo and Hayward 1982, Russel 1990, Longton 1992, Hogg et al. 1994), potentially leading to increased N supply in the canopy (Chapter 6). Because a number of vascular epiphytes are characterized by a relatively low capacity for ion uptake (e.g., Orchidaceae: Benzing 1989, 1990, Hew et al. 1993) and relatively low growth rates, increased N deposition and relatively rapid rates of N cycling in the canopy could favor species that have a greater capacity to alter NPP as a result of changes in N availability. The effects of increased N deposition on the: (i) NPP and N status of epiphytic bryophytes, (ii) rates of N cycling in the canopy, and (iii) structure of diverse epiphyte communities in TMCF await further investigation.

CHAPTER 4
NET RETENTION OF INORGANIC NITROGEN IN WET DEPOSITION BY EPIPHYTIC BRYOPHYTES, EPIPHYTE ASSEMBLAGES AND VASCULAR PLANT FOLIAGE

Introduction

Deposition of nitrate (NO_3^-) and ammonium (NH_4^+) from the atmosphere occurs in two forms: (i) "wet deposition" which includes the impaction and sedimentation of cloud water and precipitation, and (ii) "dry deposition" which includes the impaction of gases (NO_x, NH_3) and vapors (HNO_3), and the impaction and sedimentation of particles containing NO_3^- or NH_4^+ (Lovett and Lindberg 1993, Sutton et al. 1993). Understanding the functional significance of epiphytic bryophytes in the N cycle of tropical montane cloud forests (TMCF) requires an evaluation of their effects on inorganic N in wet deposition, because it is likely the dominant pathway of N deposition to these ecosystems (Vogelmann 1973, Cavelier and Goldstein 1989, McDowell and Asbury 1993). A number of investigations have demonstrated the ability of terrestrial bryophytes to retain and assimilate inorganic N from solutions and precipitation (Rieley et al. 1979, Weber and Van Cleve 1984, Woodin and Lee 1987, Urban et al. 1988, Bowden 1991), and it is likely that epiphytic bryophytes also retain and assimilate inorganic N from wet deposition because the majority of epiphytic bryophytes in TMCF are physiologically similar to ectohydric terrestrial bryophytes (i.e., they lack a well-developed cuticle and are poikilohydric). However, rates of inorganic N retention by epiphytic bryophytes from the various forms of wet deposition occurring in TMCF have not been measured.

Information concerning the effects of complex epiphyte assemblages and vascular plant foliage in TMCF on inorganic N inputs in wet deposition is also lacking. Nadkarni (1986a) reported that assemblages of epiphytic bryophytes, vascular epiphytes and DOM retained N from precipitation during the dry season, and that net leaching of N from assemblages occurred during the wet season, but did not report separate results for NO_3^- and NH_4^+. Coxson (1991) reported substantial net leaching of N from desiccated assemblages of epiphytic bryophytes and DOM when they were exposed to intense precipitation at a TMCF in Guadeloupe, but did not investigate retention of inorganic N from wet deposition. Vascular plant foliage in TMCF is typically characterized by a thick, waxy cuticle, thus the effects of this canopy component on inorganic N inputs in wet deposition are presumed to be minimal.

The objectives of this study were to investigate the effects of (i) epiphytic bryophytes, (ii) epiphyte assemblages consisting of epiphytic bryophytes, vascular epiphytes and DOM, (iii) vascular epiphyte foliage, and (iv) host tree foliage on NO_3^- and NH_4^+ additions in artificial cloud water and precipitation solutions.

Methods and Materials

General Approach

Four representative canopy components were exposed to artificial solutions, and NO_3^- and NH_4^+ concentrations were determined in the leachates. Components were: (i) epiphytic bryophytes, (ii) assemblages of epiphytic bryophytes, vascular epiphytes and DOM, (iii) vascular epiphyte foliage, and (iv) host tree foliage. Application rates and concentrations of NO_3^-, NH_4^+, and other major ions in artificial solutions were within the range of those occurring in cloud water and precipitation at the field site (Appendix B). Leaching experiments using epiphytic bryophytes were followed by deionized (DI-) water rinses, and NO_3^- and NH_4^+ concentrations were determined in these leachates.

Epiphytic Bryophytes

Shoots of the common life-forms of epiphytic bryophytes (pendants, fans, tails, mats, wefts, turfs, and cushions; life-form terminology sensu Mägdefrau 1982, During 1992) and their accumulated litter were exposed to cloud water, mist, or precipitation solutions followed by DI-water rinses in the laboratory. Samples were collected from the canopies of seven trees and ten recent treefalls (<2 weeks old) at the field site and transported to the laboratory in new polyethylene bags where they were sorted into four groups: (i) pendants, (ii) fans + tails, (iii) mats + wefts, and (iv) turfs + cushions. Life-forms were pooled into groups because they frequently co-occur in the canopy. Samples were placed in polypropylene funnels (pendants, fans + tails) or Buchner funnels (mats + wefts, turfs + cushions) attached to polypropylene bottles that had been washed in 0.1M HCl and rinsed 5 times with DI-water. Shoot densities of samples in the funnels closely approximated those occurring in the field. Each life-form group was replicated five times and fresh samples were used for each leaching experiment.

Analytical grade reagents and DI-water were used to prepare artificial cloud water (CW), mist (MIST), and three contrasting precipitation solutions (PRE1, PRE2, PRE3)(Table 4-1). Cloud water and mist solutions were applied with a manual pump sprayer, and precipitation solutions were applied with a watering bottle. Solutions were applied to each sample for ca. 2 minutes at 15 or 30 minute intervals. Ambient air temperatures ranged between 18 °C and 23 °C. Ambient light intensity and relative humidity levels were not controlled but were similar for all experiments. At the end of each experiment, leachates were measured for volume and filtered with Gelman 0.45 μ GF/A filters using a polypropylene syringe. Filtered samples were then stored at 4 °C until analyzed (< 2 weeks).

Table 4-1. Inorganic N concentrations, application rates, duration, and inorganic N additions for the artificial cloud water (CW), mist (MIST), and precipitation (PRE1, PRE2, PRE3) solutions applied to epiphytic bryophytes.

N Concentrations and Conditions	Experiment				
	CW	MIST	PRE1	PRE2	PRE3
[NO_3^- -N] (mg l^{-1})	1.16	0.45	0.10	0.06	0.01
[NH_4^+ -N] (mg l^{-1})	1.35	0.41	0.09	0.06	0.02
Application Rate (mm hr^{-1})	0.5	1	5	10	10
Duration (hours)	8	8	4	4	4
N addition (μg N $sample^{-1}$)	99.8	71.6	36.5	47.5	10.7

Epiphytic bryophyte samples were rinsed with DI-water 36 to 48 hours after exposure to CW, MIST or PRE solutions. DI-water was applied with a watering bottle at a rate of 1 cm hr^{-1} for 2 hours, and leachates were collected in 0.1 M HCl washed and DI-water rinsed polyethylene bottles. Leachates were filtered and stored using the protocol above until analyzed. Samples were dried at 60 °C for 48 hr and weighed. The mean sample mass for all experiments was 2.41 ± 0.39 g (mean g dry wt. ± 1 s.d., n=25) for pendants, 2.41 ± 0.62 g (n=25) for fans + tails, 3.26 ± 0.59 g (n=25) for mats + wefts, and 4.45 ± 0.53 g (n=25) for turfs + cushions.

Epiphyte Assemblages

Epiphyte assemblages consisting of epiphytic bryophytes, vascular epiphytes and DOM were exposed to artificial cloud water, mist or precipitation solutions in the laboratory. Samples were collected from three trees at the field site and transported to the laboratory in new polypropylene bags where they were placed in Buchner funnels attached to polypropylene bottles that had been washed in 0.1M HCl and rinsed 5 times with DI-water. Samples were replicated five times and fresh samples were used for each leaching experiment.

Artificial CW, MIST, and two precipitation solutions (PRE1, PRE2) were prepared and applied to samples in a similar manner as in the leaching experiments described above (Table 4-2). Ambient air temperatures, light intensity, and relative humidity levels were similar among experiments. Leachates were measured for volume, filtered, and stored using the protocol above. Samples were dried at 60 °C for 48 hr, separated into initially live bryophyte shoots, bryophyte litter, humus, vascular plant shoots, and roots, and then weighed. The mean sample mass for all leaching experiments was 8.51 ± 2.55 g (mean g dry wt. ± 1 s.d., n=20). Samples were composed of 35% to 65% DOM (litter + humus) by mass.

Vascular Epiphyte Foliage

Foliage and stem samples of two abundant vascular epiphytes (*Disterigma humboldtii* (Kl.) Ndzu.; Ericaceae and *Pluerothallis ruscufolia* (Jacq.) R. Br.; Orchidaceae) were exposed to artificial cloud water or mist solutions in the laboratory. Intact samples including roots and DOM were collected from three trees at the field site and immediately transported to the laboratory in new polypropylene bags. Samples were placed in styrene pots, and roots and DOM were saturated with DI-water. Acrylic plastic trays (12 cm x 12 cm base, 8 cm tall) with Parafilm sleeves were fitted around the stems of each sample to collect leachates from foliage and stem surfaces only. Samples were replicated five times, and fresh samples were used for each experiment.

Table 4-2. Inorganic N concentrations, application rates, duration, and inorganic N additions for the artificial cloud water (CW), mist (MIST), and precipitation (PRE1, PRE2) solutions applied to epiphyte assemblages consisting of epiphytic bryophytes, vascular epiphytes and DOM.

N Concentrations and Conditions	Experiment			
	CW	MIST	PRE1	PRE2
[NO_3^- -N] (mg l^{-1})	1.15	0.62	0.12	0.04
[NH_4^+ -N] (mg l^{-1})	1.36	0.12	0.12	0.05
Application Rate (mm hr^{-1})	0.5	1.8	13.0	8.2
Duration (hours)	8	4	4	4
N addition (μg N $sample^{-1}$)	100.4	59.2	124.8	29.5

Artificial cloud water (CW) and mist (MIST) solutions were prepared and applied in a similar manner as in the leaching experiments described above (Table 4-3). Ambient air temperatures, light intensity, and relative humidity levels were similar among experiments. Leachates were measured, filtered, and stored using the protocol above. Foliage and stem samples were separated from roots and DOM, dried at 60 °C for 48 hr, and then weighed. Mean sample mass for both experiments was 1.53 ± 0.55 g (mean g dry wt ± 1 s.d., n=10) for *Disterigma* and 1.89 ± 0.35 g (n=10) for *Pleurothallis*.

Host Tree Foliage

Mature foliage and twigs of the three most abundant tree species in the canopy (*Ocotea tonduzii* Standley; Lauraceae, *Ficus tuerckheimii* Standley; Moraceae, and *Meliosma ideopoda* S.F.Blake; Sabiaceae) were exposed *in situ* to artificial cloud water or mist solutions at the field site. Samples were accessed from a 27 m meteorological tower (*Ocotea*), or by using modified rock climbing techniques to gain access to mid-canopy locations (*Ficus*, *Meliosma*). Shoots were replicated five times for *Ocotea* and *Ficus*, and 3 times for *Meliosma*. Fresh shoots were used for each leaching experiment.

Artificial CW and MIST solutions were prepared and applied in a similar manner as described above (Table 4-4). Leachates were collected with polypropylene funnels

Table 4-3. Inorganic N concentrations, application rates, duration, and inorganic N additions for the artificial cloud water (CW) and mist (MIST) solutions applied to vascular epiphyte foliage and stems.

N Concentrations and Conditions	Experiment	
	CW	MIST
[NO_3^- -N] (mg l^{-1})	1.32	0.32
[NH_4^+ -N] (mg l^{-1})	0.81	0.28
Application Rate (mm hr^{-1} ± 1 s.d.)	0.23 ± 0.08	0.88 ± 0.36
Duration (hours)	8	4
N addition (μg N $sample^{-1}$ ± 1 s.d.)	39.5 ± 14.0	21.0 ± 8.6

Table 4-4. Inorganic N concentrations, application rates, duration, and inorganic N additions for the artificial cloud water (CW) and mist (MIST) solutions applied to host tree foliage and twigs.

Conditions and Ion Concentrations	Experiment	
	CW	MIST
$[NO_3^- -N]$ $(mg\ l^{-1})$	1.14	0.46
$[NH_4^+ -N]$ $(mg\ l^{-1})$	1.44	0.39
Application Rate (mm hr^{-1} ± 1 s.d.)	0.38 ± 0.11	0.87 ± 0.27
Duration (hours)	4	4
N addition (μg N $sample^{-1}$ ± 1 s.d.)	39.4 ± 11.8	29.9 ± 9.0

(16.2 or 19.5 cm dia.) that had been washed in 0.1 M HCl and rinsed 5 times with DI-water mounted beneath samples. Ambient conditions were daytime, overcast, and high relative humidity (>90%) with no precipitation. Leachates were measured, filtered, and stored using the protocol above. Shoots were harvested and leaf areas were determined graphically. Mean leaf areas for both leaching experiments were 2.4 ± 0.7 (mean dm^2 dm^{-2} ± 1 s.d., n=10) for Ocotea, 2.2 ± 0.4 (n=10) for Ficus, and 2.3 ± 0.3 (n=6) for Meliosma.

Chemical Analyses

Artificial cloud water, mist and precipitation solutions, leachates from solution additions, and leachates from DI-water rinses were analyzed for NO_3^- and NH_4^+ as described in Appendix A.

Data Analyses

Net retention of inorganic N by components was calculated by subtracting NO_3^- -N + NH_4^+ -N amounts in leachates from those in artificial solution additions. T-tests were used to detect net retention or leaching of inorganic N by components, and to detect differences in the net retention or leaching of added NO_3^- vs. NH_4^+. One-way ANOVA and Tukey Honestly Significant Difference multiple comparisons were used to detect differences in retention or leaching among life-form groups of bryophytes and to detect differences in the proportions of inorganic N retained as a function of N additions in cloud water and mist solutions among components. Homogeneity of group variances was tested with Bartlett's test and values were log-transformed and retested where necessary. Kruskal-Wallace and Wilcoxon two-sample nonparametric tests were used where transformations failed to produce homogeneous group variances. SYSTAT statistical packages (Wilkinson 1987) were used for all statistical analyses.

Results

Epiphytic Bryophytes

Epiphytic bryophytes retained inorganic N from CW, MIST and PRE1 solutions (T-tests, $P < 0.001$), but not from PRE2 and PRE3 solutions (Figure 4-1). Mean net retention from CW, MIST and PRE1 solutions represented 93%, 86% and 59% of the inorganic N additions, respectively. Epiphytic bryophytes retained a greater proportion of the NH_4^+ -N additions when compared to NO_3^- -N additions in CW and PRE1 solutions (paired-sample T-tests, $P < 0.05$)(Table 4-5). Differences in the net retention of inorganic N were detected among the life-form groups on a per gram dry weight basis with the CW, MIST and PRE1 solutions; pendants and fans + tails generally retained greater amounts of N than

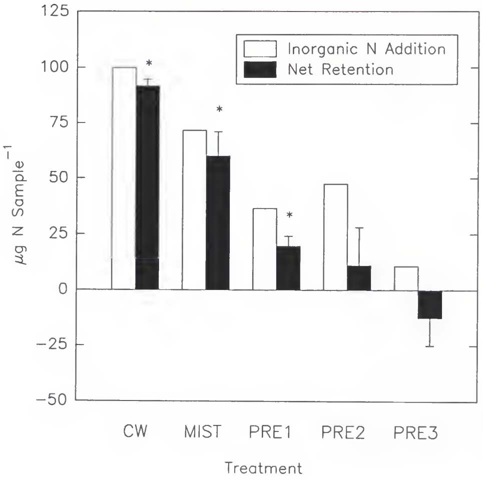

Figure 4-1. Inorganic N (NO_3^- -N + NH_4^+ -N) addition (open bars) and net retention of inorganic N (closed bars) by epiphytic bryophytes from artificial cloud water, mist or precipitation solutions (mean ± 1 s.d., * = $P < 0.05$).

Table 4-5. Percent (mean % ± 1 .d.) net retention (positive values) or net release (negative values) of NO_3^- -N and NH_4^+ -N additions by epiphytic bryophytes from artificial cloud water, mist and precipitation solutions.

Treatment	% N Retention or Release ± 1 s.d.	
	NO_3^--N	NH_4^+-N
CW	92.0 ± 5.5[a]	94.9 ± 3.4[b]
MIST	84.5 ± 10.6	81.3 ± 25.5
PRE1	49.2 ± 14.4[a]	68.3 ± 12.4[b]
PRE2	34.4 ± 16.8	14.3 ± 68.1
PRE3	-10.6 ± 56.9	-211.7 ± 204.1

Different superscripts indicate significant differences between percent retention of NO_3^- -N vs. NH_4^+ -N (Paired-sample T-tests, $P < 0.05$).

mats + wefts and turfs + cushions (ANOVAs, $P < 0.05$)(Table 4-6). Leaching of inorganic N from epiphytic bryophytes by DI-water rinses following the N additions in CW and precipitation solutions was not detected, but a trend towards net NH_4^+ -N leaching was noted (Table 4-7).

Epiphyte Assemblages

Assemblages of epiphytic bryophytes, vascular epiphytes and DOM retained inorganic N from all solutions (T-tests, $P < 0.05$ to 0.07)(Figure 4-2). Mean net retention of inorganic N from CW, MIST and PRE2 solutions represented >98%, 91% and 53% of the N additions, respectively. Differences among the proportions of NO_3^- -N and NH_4^+ -N retained from solutions were not detected.

Vascular Epiphyte Foliage

A trend towards the net release of inorganic N from vascular epiphyte foliage exposed to CW solutions was detected, and net release of inorganic N was detected from vascular epiphyte foliage exposed to MIST solutions (T-test, $P < 0.05$)(Figure 4-3). Net release of inorganic N represented 2% of N additions in CW solutions and 39% of N additions in MIST solutions. Net release of NH_4^+ -N accounted for nearly all of the inorganic N released from vascular epiphyte foliage exposed to MIST solutions (paired-sample T-test, $P < 0.001$).

Table 4-6. Net retention (positive values) or net release (negative values) of inorganic N (mean μg NO_3^- -N + NH_4^+ -N (g dry wt)$^{-1}$ ± 1 s.d.) by epiphytic bryophytes from artificial cloud water, mist and precipitation solutions (n=5 for each life-form group).

Treatment	Net Retention (+) or Release (-) mean μg (NO_3^- -N + NH_4^+ -N) (g dry wt)$^{-1}$ ± 1 s.d.			
	Pendants	Fans + Tails	Mats + Wefts	Cushions + Turfs
CW	43.7 ± 6.3^{a}	38.0 ± 2.5^{a}	26.7 ± 4.0^{b}	20.5 ± 3.8^{b}
MIST	21.2 ± 6.7^{ac}	25.8 ± 3.9^{a}	18.6 ± 2.0^{bc}	13.6 ± 1.0^{b}
PRE1	9.1 ± 0.9^{a}	12.0 ± 2.1^{a}	10.0 ± 2.6^{b}	5.6 ± 0.9^{b}
PRE2	0.3 ± 5.5	5.7 ± 2.9	7.9 ± 2.4	0.5 ± 7.7
PRE3	-7.9 ± 3.5	-6.6 ± 7.3	-1.8 ± 1.8	-1.7 ± 1.2

Different superscripts indicate significant differences between life-forms ($ANOVA_{3,16}$, $P < 0.05$).

Table 4-7. Leaching of NO_3^- -N, NH_4^+ -N, and inorganic N (mean μg N sample^{-1} ± 1 s.d.) from epiphytic bryophytes by DI-water rinses following exposure to artificial cloud water, mist, or precipitation solutions.

Treatment	Amount of N Leached μg N sample^{-1} ± 1 s.d.		
	NO_3^- -N	NH_4^+ -N	Inorganic N
CW	1.1 ± 1.2	4.8 ± 2.4	5.9 ± 3.2
MIST	1.1 ± 0.4	5.6 ± 5.5	6.7 ± 5.7
PRE1	0.5 ± 0.2	3.0 ± 1.8	3.0 ± 1.8
PRE2	1.1 ± 1.4	17.6 ± 24.4	19.7 ± 26.4
PRE3	0.9 ± 0.8	5.9 ± 3.1	6.8 ± 3.2
Mean of Treatments	0.9 ± 0.9	7.3 ± 11.8	8.1 ± 12.2

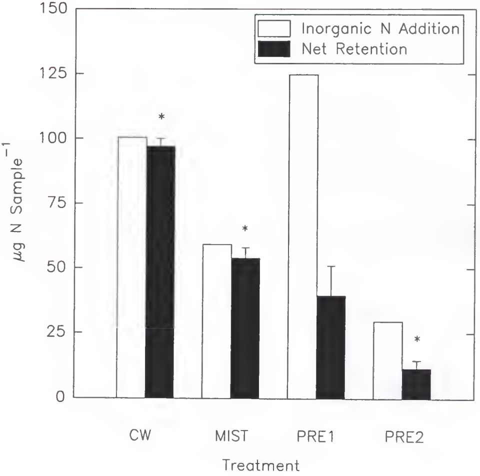

Figure 4-2. Inorganic N (NO_3^- -N + NH_4^+ -N) addition (open bars) and net retention of inorganic N (closed bars) by assemblages of epiphytic bryophytes, vascular epiphytes and DOM from artificial cloud water, mist or precipitation solutions (mean ± 1 s.d., * = $P < 0.05$).

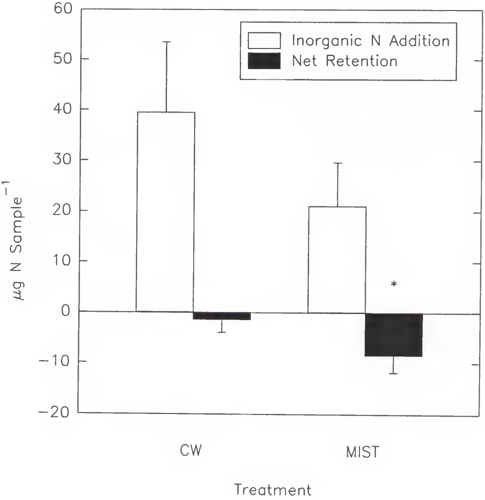

Figure 4-3. Inorganic N (NO_3^- -N + NH_4^+ -N) addition (open bars) and net retention of inorganic N (closed bars) by vascular epiphyte foliage from artificial cloud water or mist solutions (mean ± 1 s.d., * = $P < 0.05$).

Host Tree Foliage

Net inorganic N retention by host tree foliage from CW and MIST solutions was not detected, but there was a trend towards net NH_4^+ -N retention by foliage from CW solutions (Figure 4-4). Mean net retention of inorganic N from CW and MIST solutions represented only 9% and 5% of the N additions, respectively.

Comparisons Among Canopy Components

Epiphytic bryophytes and epiphyte assemblages retained greater proportions of the inorganic N additions in CW solutions when compared to vascular plant foliage (Kruskal-Wallis nonparametric test, $H_3 = 39.32$, $P < 0.001$). Differences in the proportions of inorganic N additions retained among epiphytic bryophytes and epiphyte assemblages were not detected with CW solutions. Differences in the proportions of inorganic N retained from MIST solutions were also detected among canopy components (ANOVA, $F_{3,44} = 214.029$, $P < 0.001$). Epiphytic bryophytes and epiphyte assemblages retained similar proportions of the N additions in MIST solutions, and greater proportions than vascular plant foliage. Proportions of net N retention by host tree foliage from MIST solutions were greater when compared to vascular epiphyte foliage (Tukey HSD, $P < 0.05$).

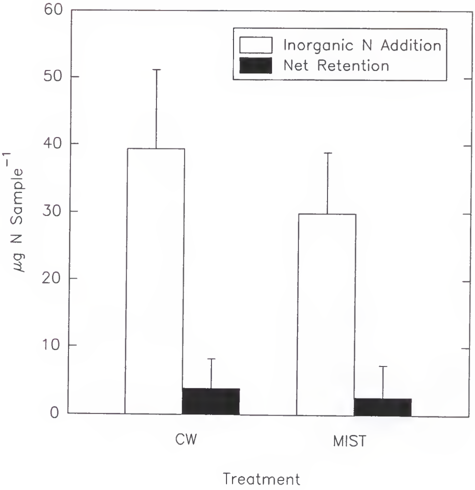

Figure 4-4. Inorganic N (NO_3^- -N + NH_4^+ -N) addition (open bars) and net retention of inorganic N (closed bars) by host tree foliage from artificial cloud water or mist solutions (mean ± 1 s.d.).

Discussion

Epiphytic Bryophytes

The relatively large solution storage capacities of epiphytic bryophytes (4 to 7 g H_2O (g dry wt)$^{-1}$; Pócs 1982, Veneklaas et al. 1990, Chapter 5) and their lack of a well-developed cuticle resulted in relatively long residence times of the CW, MIST and PRE1 solutions adjacent to cell walls and metabolically active tissues when compared to the PRE2 and PRE3 solutions. In this context, net retention of inorganic N was likely due to the development of relatively steep concentration gradients at cell walls and across membranes, facilitating ion exchange and assimilation (Neiboer et al. 1978, Richardson 1981, Richter and Dainty 1989a, Schaefer and Reiners 1990). Subsequent evaporation following exposure to these solutions may have further steepened concentration gradients.

The majority of NO_3^- retained by epiphytic bryophytes was apparently assimilated, because minimal amounts of NO_3^- were leached by the subsequent DI-water rinses. Net leaching of NO_3^- by DI-water rinses represented < 11% of the NO_3^- retained from CW, MIST, and PRE1 solutions. Net leaching of NH_4^+ from epiphytic bryophytes exposed to PRE2 and PRE3 solutions and DI-water rinses, although non-significant, were likely due to the exchange of NH_4^+ from cation exchange sites on cell walls or leaching of NH_4^+ from accumulated litter (Chapter 6).

Differences in net inorganic N retention among the life-form groups on a per gram dry weight basis may have been due to different biomass values among groups (ANOVA, $F_{3,93}=75.591$, $P < 0.001$; pendants = fans + tails < mats + wefts < cushions + turfs). Samples of these latter two groups consisted of a larger proportion of older shoots and accumulated litter which apparently have a lower capacity to retain inorganic N than younger shoots (K. Clark, unpub. data). It is also possible that pendants, fans, and tails, which typically occur in the upper canopy, have a greater capacity to retain inorganic N from solutions when concentrations are relatively high.

Net inorganic N retention by epiphytic bryophytes is similar to results reported for terrestrial bryophytes from cool temperate and boreal ecosystems. Woodin and Lee (1987) demonstrated that Sphagnum fuscum from a subarctic bog retained >95% of the NO_3^- in bulk precipitation in the field, and from 55% to 90% of the NO_3^- loadings during laboratory leaching experiments. Bowden (1991) used both bulk precipitation and an artificial precipitation treatment to demonstrate inorganic N retention by Polytrichum spp. in an early successional ecosystem. He reported that 95% of the N additions in bulk precipitation and 96% of those in artificial precipitation were retained. The retention rate of NO_3^- by Sphagnum magellanicum reported by Urban et al. (1988) was in the range of our results for CW and MIST solutions: 2.1 μg NO_3^- -N g dry wt^{-1} hr^{-1} in a solution containing 0.72 mg NO_3^- -N l^{-1}.

Nitrate assimilation by Sphagnum spp. is apparently due to the activity of non-inducible carriers (Diesing and Rudolf 1987). Sphagnum spp. show inducible as well as constitutive nitrate reductase activity when exposed to NO_3^- in solution (Woodin et al. 1985, Diesing and Rudolf 1988) and in atmospheric deposition (Woodin and Lee 1987, Lee et al. 1990), as do a number of species of epiphytic bryophytes (K. Clark and N. Nadkarni, unpub. data). The relatively large amounts of cell wall material in epiphytic bryophytes may play a role in the retention of NH_4^+, and NH_4^+ may be taken up passively along favorable electrochemical gradients (Neiboer et al. 1978). The NH_4^+ assimilating enzymes, glutamine synthetase and glutamate synthase, have been detected in a number of bryophytes (Meade 1984).

Epiphyte Assemblages

The low rates of solution addition to assemblages of epiphytic bryophytes, vascular epiphytes and DOM during the CW and MIST experiments also resulted in relatively long residence times of these solutions adjacent to cell walls and metabolically active tissues, including intact fine roots of vascular epiphytes. Solutions first percolated through live shoots of epiphytic bryophytes, so it is likely that they retained a substantial portion of the inorganic N additions. Fine roots of vascular epiphytes were observed in all samples and they may have also contributed to the observed net retention of inorganic N. When samples of DOM only were exposed to MIST solutions (K. Clark, unpub. data), some inorganic N was retained, presumably due to N immobilization by microbial populations (Vance and Nadkarni 1990, Davidson et al. 1990, 1992). The relative importance of bryophytes, fine roots and microbial biomass in the retention and assimilation of inorganic N by epiphyte assemblages requires further investigation.

Vascular Plant Foliage

In contrast to the patterns of net N retention observed for epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes and DOM, vascular plant foliage retained minimal amounts of inorganic N from CW and MIST solutions. The failure of vascular foliage to retain N from these solutions was likely due to (i) the relatively small volumes of solution stored on foliar surfaces (Herwitz 1985), (ii) the presence of a relatively thick, waxy cuticle on foliar surfaces that apparently has a high resistance to solution penetration to leaf mesophyll tissue (Lovett et al. 1989, Schaefer and Reiners 1990), and (iii) apparently minimal solution penetration through stomates to leaf mesophyll tissue. Net release of NH_4^+ from vascular epiphytes may have been due to the leaching of necrotic areas on foliage and bracts on some of the samples.

Other investigations involving leaching of vascular plant foliage have generally shown similar patterns to those reported here and have demonstrated uptake of NH_4^+ but little uptake of NO_3^- from artificial cloud water and precipitation solutions. For example, new and old foliage of Abies balsamea retained some NH_4^+ but little NO_3^- when exposed to an artificial precipitation solution (1.31 mg NH_4^+ -N l^{-1}, 0.32 mg NO_3^- -N l^{-1}) at a range of application rates (3 to 35 mm hr^{-1})(Reiners and Olson 1984). Bowden et al. (1989) reported greater uptake of $^{15}NH_4^+$ than of $^{15}NO_3^-$ by young foliage of Picea rubens exposed to mistings of artificial cloud water (2.0 mg NH_4^+ -N or NO_3^- -N l^{-1}). Garten and Hanson (1990) found that foliage of Quercus alba and Acer rubra absorbed some $^{15}NH_4^+$ but little $^{15}NO_3^-$ from artificial precipitation (1.71 mg NH_4^+ -N l^{-1}, 0.79 mg NO_3^- -N l^{-1}). Application rates were not reported in these latter two investigations, thus direct comparisons to my results are difficult. Similar results have also been reported for Picea abies (Wilson 1992, Lumme 1994) and Pinus sylvestris (Wilson 1992).

When foliage of Acer rubra was damaged artificially and cuticles were disrupted, net retention rates of NO_3^- and NH_4^+ from artificial precipitation were increased over those characterizing undamaged foliage, further suggesting that cuticular resistance to solution penetration is important in controlling net N retention by foliage of vascular plants (Potter 1991).

These results suggest that epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes, and DOM retain inorganic N from relatively N-enriched solutions, and support the hypothesis that wet deposition is an important source of N for epiphytic vegetation in TMCF (Nadkarni 1984, Benzing 1981, 1990). It is likely that inorganic N is initially retained and assimilated by epiphytic bryophytes and other epiphytes with minimal cuticular protection, and then becomes available to vascular epiphytes via the leaching and net mineralization of primarily NH_4^+ -N from DOM (Vance and Nadkarni 1990, Coxson 1991, Chapter 6). Although some vascular epiphytes have evolved specialized adaptations or interactions with other organisms to acquire nutrients (e.g., tanks, insect traps, myrmecorous shoots)(Huxley 1980, Benzing 1989, 1990, Davidson and Epstein 1989), fine roots are probably the major absorptive organ for the majority of vascular epiphytes that have a relatively thick, waxy cuticle on foliar surfaces (Benzing 1990, Hew et al. 1993). In this respect, the functioning of epiphytic bryophytes is similar to that of terrestrial bryophytes in ecosystems where they are abundant: because of their ability to assimilate inorganic N from atmospheric deposition, N_2- fixation and other sources, bryophytes may regulate rates of N cycling and thus N availability in the canopy via control over the processes of N leaching and net N mineralization from DOM

(Oechel and Van Cleve 1986, Urban and Eisenreich 1988, Verhoeven et al. 1990, Longton 1992).

In addition to their roles in the accumulation and storage of N in the canopy and in litterfall inputs to the forest floor in TMCF (Pocs 1982, Nadkarni 1984, Nadkarni and Matelson 1992a, Chapter 3), these results suggest that epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes and DOM alter inorganic N fluxes in throughfall and stemflow. These components display a large surface area in the canopy and are able to intercept cloud water, mist, and precipitation as solutions pass through the canopy. Because vascular plant foliage characterizing this site apparently has a minor effect on inorganic N in solution, net retention of inorganic N by the canopy from wet deposition may be largely regulated by epiphytic components. A close correspondence exists between the patterns of net inorganic N retention by epiphytic bryophytes and epiphyte assemblages reported here and the patterns of net N retention by the canopy monitored at the site with a cloud water, precipitation and throughfall network (Clark and Nadkarni 1990, Clark et al. 1993, Appendix C). This relationship suggests that epiphytes play major roles in regulating fluxes of inorganic N from the atmosphere to the forest floor in TMCF.

CHAPTER 5

MODELLING THE EFFECTS OF EPIPHYTIC BRYOPHYTES, EPIPHYTE ASSEMBLAGES, AND VASCULAR PLANT FOLIAGE ON INORGANIC NITROGEN IN WET DEPOSITION TO A CLOUD FOREST CANOPY

Introduction

The net effect of a forest canopy on inorganic nitrogen (N) deposition from the atmosphere is typically calculated by comparing an estimate of total (wet + dry + cloud) deposition to inorganic N fluxes in throughfall and stemflow (TH+ST). Using this approach, recent ecosystem level investigations in temperate forests have indicated that most forest canopies retain inorganic N from atmospheric deposition, and that rates of inorganic N retention by the canopy are a function of deposition rates (Lovett and Lindberg 1993). Highest rates of inorganic N retention by the canopy have been reported from montane forest sites that were exposed to significant cloud water inputs (Johnson et al. 1991, Lovett and Lindberg 1993, Miller et al. 1993b).

Process-level investigations have elucidated mechanisms of canopy uptake and leaching of inorganic N and have recognized the importance of solution residence times and diffusion gradients across canopy surfaces in controlling rates of inorganic N retention (Schaefer et al. 1988, Lovett et al. 1989, Wilson 1992). Related investigations have focused on estimating rates of inorganic N retention by representative canopy components from atmospheric deposition and have determined that: (i) foliage of both coniferous and broad-leaved species retain inorganic N from cloud water and precipitation (Reiners and Olson 1984, Bowden et al. 1989, Garten and Hanson 1990, Wilson 1992, Lumme 1994), (ii) epiphytic lichens on twig and branch surfaces retain inorganic N from cloud water and precipitation (Reiners and Olson 1984), (iii) rates of inorganic N retention by epiphytic lichens are typically greater than those characterizing vascular plant foliage on a unit surface area basis (Reiners and Olson 1984), and (iv) net retention rates of ammonium (NH_4^+) -N are generally greater than those for nitrate (NO_3^-) -N for both vascular and non-vascular canopy components.

Ecosystem and process-level investigations have been less numerous in TMCF. Research efforts to date have determined that: (i) epiphyte-laden canopies retain a large proportion of inorganic N in atmospheric deposition (Asbury et al. 1988, Clark et al. 1993, McDowell and Asbury 1993, Appendix 3), (ii) epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes and dead organic matter (DOM) retain both NO_3^--N and NH_4^+ -N from cloud water and precipitation (Clark and Nadkarni 1990, 1992, Chapter 4), and (iii) vascular plant foliage retains some NH_4^+ -N but little NO_3^- -N from cloud water and precipitation (Chapter 4).

These investigations have been invaluable in the estimation and interpretation of patterns of net N retention by forest canopies. Unfortunately, relatively few studies have attempted to integrate ecosystem and process-level measurements to estimate the relative roles of canopy components in regulating inorganic N fluxes in throughfall and stemflow (Reiners and Olson 1984, Schaefer et al. 1988, Lovett et al. 1989), and none to date has addressed tropical cloud forest ecosystems. However, simulation models are a powerful tool for evaluating the importance of individual canopy components in the retention of inorganic N in atmospheric deposition to the canopy and may contribute to an understanding of the potential effects of increased N deposition to cloud forest ecosystems.

In this investigation, a simulation approach was used to model the effects of representative canopy components on inorganic N inputs in wet deposition to the canopy. The objectives were to (i) develop and evaluate a canopy hydrology and inorganic N flux model that integrated a relatively simple model of canopy structure with the results of leaching experiments that used representative canopy components, (ii) determine the importance of selected parameters on predicted hydrologic and inorganic N fluxes to the forest floor, (iii) estimate the roles that representative canopy components play in the observed net retention of inorganic N from wet deposition by the canopy, and

(iv) determine which canopy components may potentially be affected by increased N deposition to TMCF ecosystems.

Methods and Materials

Model Overview

The model developed here is based on the Rutter and Penman-Montieth models and simulates the net effects of representative canopy components on hydrologic and inorganic N inputs to the canopy in cloud water and precipitation at a time-step of one hour. The model is driven by hourly meteorological data and mean NO_3^- -N and NH_4^+ -N concentrations in cloud water and precipitation. Canopy structure and epiphyte mass were estimated from measurements and destructive sampling at the field site. A running balance of solution storage by each canopy component is calculated as a function of inputs in cloud water, precipitation and drainage from other components, and outputs via evaporation and drainage. Net retention of NO_3^- -N and NH_4^+ -N by each component is calculated as a function of the N mass in stored solutions and component-specific diffusional resistances to net NO_3^- -N and NH_4^+ -N retention derived from laboratory and field leaching experiments (Chapter 4). Solution drainage from components and non-intercepted cloud water and precipitation are summed at each time-step to calculate hydrologic, NO_3^- -N and NH_4^+ -N fluxes to the forest floor in TF. Hydrologic and inorganic N fluxes in stemflow are not simulated by the model, but a portion of the drainage from each component is diverted to stems.

Canopy Structure

Canopy structure, epiphyte mass and projected surface area estimates of canopy components were derived from measurements and destructive sampling at the field site (Ingram and Nadkarni 1993, Nadkarni et al. unpub. data) (Table 5-1). Canopy height is 15-32 m, with a mean height of about 23 m. Projected leaf area of vascular plant foliage has been estimated to be 6 m^2 m^{-2}, consistent with estimates from other tropical montane forests (3.0 to 6.4 m^2 m^{-2}; Brun 1976, Edwards and Grubb 1977, Grubb 1977, Weaver and Murphy 1990). Epiphyte mass on twigs and branches is estimated at ca. 2,000 g m^{-2}, 60% of the total epiphyte mass at the site (Vance and Nadkarni 1992, Nadkarni et al. 1993, Table 1-1). The remaining epiphyte mass occurs on branch junctions with stems and on mainstems, and so has a presumably negligible effect on throughfall fluxes.

In the model, the canopy is arranged in three layers, each composed of two components: (i) vascular plant foliage, and (ii) epiphytic vegetation and dead organic matter (DOM) (Table 5-1, Figure 5-1). Canopy components (LEAF1 and EPI1) in Layer 1 are intended to correspond to vascular plant foliage and epiphytic bryophytes and accumulated DOM on twigs and small branches in the upper and outer portions of the canopy; components (LEAF2 and EPI2) in Layer 2

Table 5-1. Estimated projected surface areas, interception areas for calculating cloud water, precipitation and drainage inputs, and mass of epiphytic canopy components per m^2 ground area used in the model.

Canopy Layer	Canopy Component	Projected Surface Area (m^2 m^{-2})	Interception Area (m^2 m^{-2})	Epiphyte Mass (g m^{-2})
1	LEAF1	3	0.778	-
	EPI1	0.5 to 0.9	0.5 to 0.9	300
2	LEAF2	2	0.632	-
	EPI2	0.2	0.2	550
3	LEAF3	1	0.393	-
	EPI3	0.1	0.1	1150
Sum		6.8 to 7.2	-	2000

Refer to Figure 5-1 for an explanation of abbreviations.

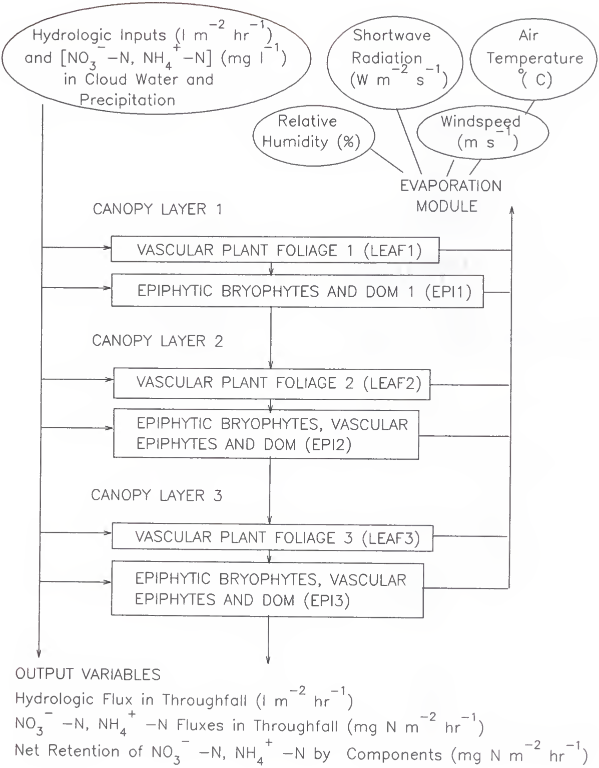
Hydrologic Inputs ($l\ m^{-2}\ hr^{-1}$) and [NO_3^-–N, NH_4^+–N] ($mg\ l^{-1}$) in Cloud Water and Precipitation
Shortwave Radiation ($W\ m^{-2}\ s^{-1}$)
Air Temperature (°C)
Relative Humidity (%)
Windspeed ($m\ s^{-1}$)
EVAPORATION MODULE
CANOPY LAYER 1
VASCULAR PLANT FOLIAGE 1 (LEAF1)
EPIPHYTIC BRYOPHYTES AND DOM 1 (EPI1)
CANOPY LAYER 2
VASCULAR PLANT FOLIAGE 2 (LEAF2)
EPIPHYTIC BRYOPHYTES, VASCULAR EPIPHYTES AND DOM (EPI2)
CANOPY LAYER 3
VASCULAR PLANT FOLIAGE 3 (LEAF3)
EPIPHYTIC BRYOPHYTES, VASCULAR EPIPHYTES AND DOM (EPI3)
OUTPUT VARIABLES
Hydrologic Flux in Throughfall ($l\ m^{-2}\ hr^{-1}$)
NO_3^- –N, NH_4^+ –N Fluxes in Throughfall ($mg\ N\ m^{-2}\ hr^{-1}$)
Net Retention of NO_3^- –N, NH_4^+ –N by Components ($mg\ N\ m^{-2}\ hr^{-1}$)

Figure 5-1. Driving variables, canopy structure and output variables of the canopy hydrology and inorganic nitrogen flux model.

correspond to vascular plant foliage and assemblages of epiphytic bryophytes, small vascular epiphytes, and DOM on medium-sized branches in the mid-canopy; and components (LEAF3 and EPI3) in Layer 3 correspond to vascular plant foliage and assemblages of epiphytic bryophytes, vascular epiphytes, and DOM on large branches in the lower canopy (Table 5-1, Figure 5-1).

Projected surface areas of vascular plant foliage components (LEAF1, LEAF2, LEAF3) in canopy Layers 1, 2, and 3 were assumed to be 3, 2, and 1 m^2 m^{-2} ground area, respectively (Table 5-1). Projected surface area of the epiphytic bryophyte and DOM component (EPI1) in canopy Layer 1 was estimated to be 0.5 m^2 m^{-2} ground area using canopy photographs and visual observations at the site. Projected surface areas of epiphytic components (EPI2, EPI3) in canopy Layers 2 and 3 were assumed to be 0.2 and 0.1 m^2 m^{-2} ground area, respectively (Table 5-1).

Model Derivation

Derivation of the canopy hydrology portion of the model followed the dynamic precipitation interception model developed by Rutter et al. (1971) for Pinus nigra in the United Kingdom. They recognized that a forest canopy has a surface water storage capacity, S, and that canopy surfaces fill with precipitation (and cloud water) and discharge via evaporation and drainage. They modelled changes in water storage on canopy surfaces as:

$$dS/dt = P * (1 - p) - E - D \qquad (1)$$

where S is the water stored on canopy surfaces (mm), P is the precipitation rate (mm hr^{-1}), p is the proportion of non-intercepted precipitation, E is the rate of evaporation (mm hr^{-1}), and D is the rate of drainage from the canopy (mm hr^{-1}). In this multi-layered canopy hydrology model, water storage by individual canopy components was treated separately (as volume per unit ground area) and equation (1) was modified to:

$$dS_x/dt = P_x + D_{x-1} - E_x - D_x \qquad (2)$$

where S_x is the water storage by canopy component x (liter m^{-2}), P_x is the interception rate of cloud water and precipitation (liter m^{-2} hr^{-1}), D_{x-1} is the interception rate of drainage from components above x (liter m^{-2} hr^{-1}), E_x is the rate of evaporation from x (liter m^{-2} hr^{-1}), and D_x is the rate of drainage from x (liter m^{-2} hr^{-1})(Figure 5-2).

Solution inputs to canopy components

Solution inputs in cloud water, precipitation and drainage from other canopy components were calculated as a function of the "interception area" of each component. Because leaf orientation is variable and leaf overlap occurs to some extent in the canopy, the interception area of vascular plant foliage is considerably less than the

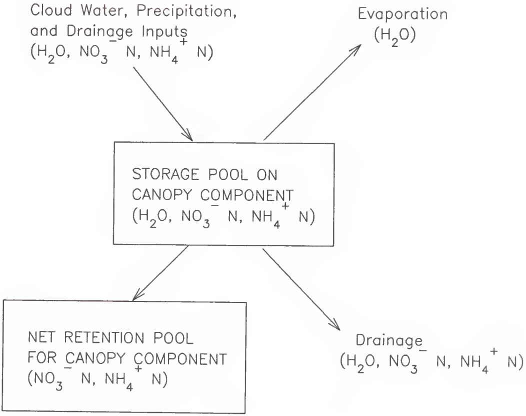
Cloud Water, Precipitation, and Drainage Inputs
(H_2O, NO_3^- N, NH_4^+ N)
Evaporation
(H_2O)
STORAGE POOL ON CANOPY COMPONENT
(H_2O, NO_3^- N, NH_4^+ N)
NET RETENTION POOL FOR CANOPY COMPONENT
(NO_3^- N, NH_4^+ N)
Drainage
(H_2O, NO_3^- N, NH_4^+ N)

Figure 5-2. State variables (boxes) and processes controlling hydrologic and inorganic N fluxes on an individual canopy component.

projected surface area. Therefore, a negative exponential relationship was used to calculate the interception areas of vascular plant foliage components (LEAF1, LEAF2, LEAF3) using their projected surface area values (Halldin et al. 1979)(Table 5-1). The interception area of epiphytic bryophytes and DOM (EPI1) in Layer 1 was assumed to be equal to the projected surface area (0.5 m^2 m^{-2}) for vertically falling droplets during convective precipitation events. During advective events, however, wind-driven cloud and precipitation combined with leaf streamlining (Montieth and Unsworth 1990) may result in greater rates of droplet penetration into the interior of the canopy and, therefore, increased interception by epiphytic components in the upper canopy. In this context, the interception area of epiphytic bryophytes and DOM (EPI1) in canopy Layer 1 is greater than that for vertically falling precipitation but was difficult to estimate accurately in the field. The interception areas of epiphytic components (EPI2, EPI3) in canopy Layer 2 and 3 were assumed to be equal to their projected surface area values because the upper canopy is the major sink for momentum (Table 5-1).

Mixing of nitrate and ammonium in solutions

Alteration of the Rutter et al. (1971) model to incorporate inorganic N fluxes in canopy solutions required two assumptions concerning the mixing of NO_3^- -N and NH_4^+ -N: (i) NO_3^- -N and NH_4^+ -N in cloud water, precipitation and drainage inputs to a canopy component were assumed to be mixed completely at each time step, and (ii) NO_3^- -N and NH_4^+ -N in solution inputs to a canopy component were assumed to be mixed completely with solutions already stored by that component at each time step (Olson et al. 1985, Lovett et al. 1989)(Figure 5-2).

Evaporation from canopy components

A potential rate of evaporation from each of the three layers in the canopy was calculated using the Penman-Monteith equation (Monteith 1965, Rutter et al. 1971, Gash et al. 1979, Monteith and Unsworth 1990). Surface temperatures of canopy components were assumed to be completely coupled to ambient air temperature (Gates 1969, Calder et al. 1986). Penetration of shortwave radiation through canopy layers was approximated as a function of cumulative projected surface area using the Beer-Lambert law, with assumed values for the surface reflectance and the light extinction coefficient of 0.12 and 0.52, respectively (Kira et al. 1969, Shuttleworth et al. 1984, Shuttleworth 1989) (Figure 5-3). Below-canopy shortwave radiation was predicted to be 5% of that above the canopy, consistent with measurements in this forest (Gholz et al., unpub. data) and similar to those in other mature wet tropical forests (Shuttleworth et al. 1984, Shuttleworth 1989)(Figure 5-3). Mean net radiation for each of the three layers was then estimated as a function of air temperature and incident

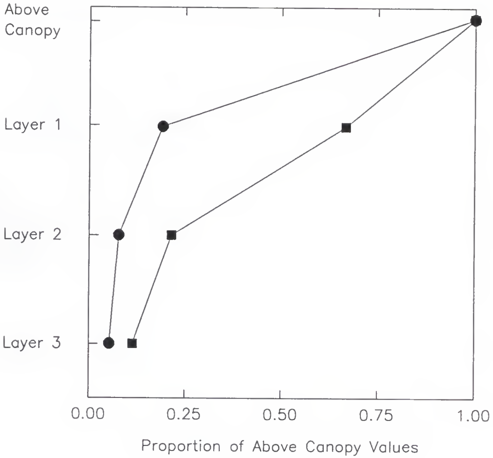

Figure 5-3. Shortwave radiation (●) above the canopy and below each canopy layer, and mean wind speed (■) above the canopy and at each canopy layer as a proportion of above-canopy values.

shortwave radiation (Rutter et al. 1981, Halldin et al. 1979, Rosenberg et al. 1983, Monteith and Unsworth 1990, Roberts et al. 1993) (Figure 5-4).

Mean windspeed at each canopy layer was approximated as an exponential decay function of windspeed above the canopy and the projected surface area of each layer in the canopy (Figure 5-3). The aerodynamic resistance to momentum, r_m, was calculated for the entire canopy using a standard formula with the zero-plane displacement d and the roughness length z_o expressed as a function of canopy height (Rutter et al. 1971, Thom 1975, Montieth and Unsworth 1990). Neutral atmospheric stability was assumed. Aerodynamic resistances to water vapor fluxes at each canopy layer were then approximated from r_m for the entire canopy as a function of mean windspeed at that layer. Therefore, it was assumed that aerodynamic resistances to momentum and water vapor flux were equivalent in the model.

Mean relative humidity at each layer was approximated as an empirical function of relative humidity measurements above the canopy; mean relative humidity increased slightly at each layer when compared to above-canopy values (Shuttleworth et al. 1985, K. Clark, unpub. data). Vapor pressure deficit at each layer was estimated from the difference between the saturation vapor pressure and the actual vapor pressure calculated from ambient air temperature and relative humidity at that layer.

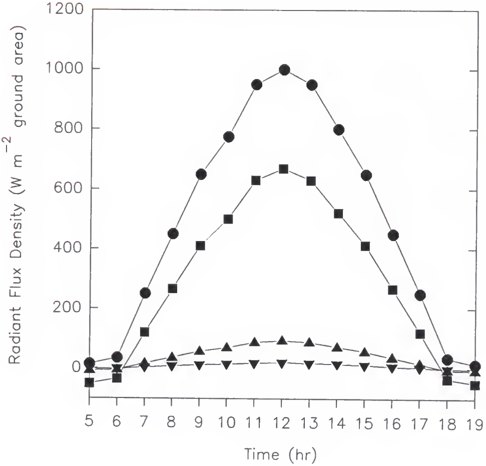

Figure 5-4. Shortwave radiation above the canopy (●) and mean net radiation at canopy Layer 1 (■), Layer 2 (▲) and Layer 3 (▼) for clear sky conditions.

The Penman-Monteith equation was then used to estimate rates of potential evaporation (liter m^{-2} hr^{-1}) from each ofthe three canopy layers (Figure 5-5). Actual rates of evaporation from canopy components in each layer were calculated by multiplying potential evaporation rates by the ratio of the projected surface area of that component to the total projected surface area in that layer and then multiplying the resultant value by a component-specific resistance term. Component-specific resistance to evaporation was assumed to be negligible when the amount of solution stored on an individual canopy component was at or beyond storage capacity (Rutter 1975, Calder and Wright 1986, Calder 1990), and was estimated by equation (3) when the amount of solution stored was below storage capacity (Rutter et al. 1971, Gash et al. 1979, Shuttleworth 1988):

$$S_x / Sc_x * \text{Weighted Potential Evaporation} \quad \text{when } S_x < Sc_x \quad (3)$$

where Sc_x = the water storage capacity of component x.

Net retention of inorganic nitrogen by canopy components

Derivation of the inorganic N flux portion of the canopy model generally followed the model of K^+ and NH_4^+ exchange developed by Lovett et al. (1989) for a Abies balsamea forest in New Hampshire. They recognized that the diffusion of NH_4^+ into canopy components was a function of concentration gradients across canopy surfaces and a surface

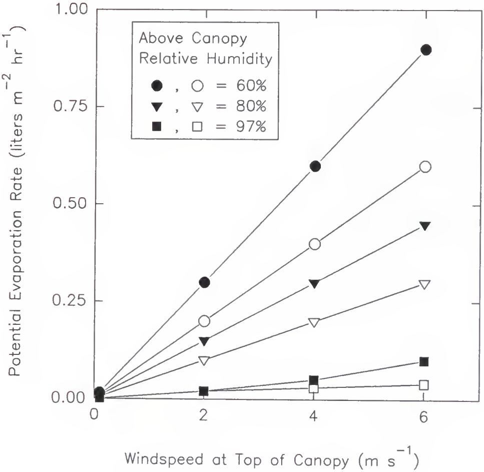

Figure 5-5. Rates of potential evaporation from the canopy as a function of windspeed and relative humidity at the top of the canopy for clear sky midday conditions (filled symbols) and cloudy midday conditions (hollow symbols).

resistance to diffusion to internal pools (Schaefer et al. 1988, Schaefer and Reiners 1990, Wilson 1992). Conceptual development leads to:

$$F_n = \{[N_{int}] - [N_{ext}]\} / r_n \qquad (4)$$

where F_n is the flux of NO_3^- -N or NH_4^+ -N across the component surface (mg dm^{-2} hr^{-1}), N_{int} and N_{ext} are the internal and external concentrations (mg $liter^{-1}$), respectively, and r_n is the resistance to NO_3^- -N or NH_4^+ -N diffusion from external to internal pools (hr dm^{-1}). Because N_{int} is assumed to be minimal due to assimilation by living cells and N_{ext} can be expressed as an amount of NO_3^- -N or NH_4^+ -N stored in solution on canopy surfaces, equation (4) is modified to:

$$F_n = - N_{ext} / S_x * r_n \qquad (5)$$

where N_{ext} is the amount of NO_3^- -N or NH_4^+ -N in solution (mg), and S_x is the solution storage by canopy component x (liter dm^{-2}). The negative value indicates net influx to the canopy component, and depletion of NO_3^- -N and NH_4^+ -N from stored solutions is calculated from the amounts retained at each time step (Figure 5-2).

Drainage from canopy components

Various equations have been proposed to calculate the rate of drainage, D, from the canopy (or canopy components).

Rutter et al. (1971) modelled drainage from a Pinus nigra canopy as:

$$D = D_o \, ß \, (C - S) \qquad (6)$$

where D_o is the rate of drainage from the canopy when C = S, ß is an empirically derived dimensionless drainage coefficient, C is the depth of water stored on the canopy, and S is the water storage capacity of the canopy. However, this formulation has been criticized, because small but finite drainage was calculated when the canopy was completely dry (Rutter and Morton 1977, Aston 1979, Massman 1980). More complex formulations where drainage rates were calculated implicitly may also be inaccurate (Erickson and Grip 1979, Massman 1983). Therefore, drainage from canopy components is modelled here explicitly as a function of solution input. Following Massman (1980), drainage from canopy components during the wetting-up phase is calculated as:

$$D_x = (P_x + D_{x-1}) * (e^{\alpha (S_x / Sc_x)} - 1) / (e^{\alpha} - 1) \qquad (7)$$

where α is a dimensionless drainage parameter. When $S_x = 0$, no drainage occurs, and when $S_x = Sc_x$, $D_x = (P_x + D_{x-1})$, thus the boundary conditions are met. Finite positive values of α predicted progressively greater rates of drainage as S approached Sc, thus equation (7) approximates a "leaky cup". Small, finite positive values of α generally predicted the wetting up of canopy surfaces accurately. When solution storage by a canopy component exceeded the storage capacity, the "excess" solution drained from the component. Therefore, drainage was modelled here explicitly as a function of solution input (Figure 5-2).

Drainage from all components was reduced using a stem drainage parameter to account for solutions diverted to stems (Lovett et al. 1989)(Figure 5-2). Hydrologic and inorganic N fluxes in stemflow were not simulated in this version of the model.

Model Variables and Flow Functions

State variables

State variables in the model are: (i) the amounts of solution (liter m^{-2} ground area), NO_3^- -N and NH_4^+ -N (mg N m^{-2} ground area) stored by each of the six canopy components, (ii) amounts of NO_3^- -N and NH_4^+ -N (mg N m^{-2} ground area) retained by each canopy component, and (iii) amounts of solution (liter m^{-2}), NO_3^- -N and NH_4^+ -N (mg N m^{-2}) in throughfall on the forest floor (Figure 5-2).

Driving variables

Hourly cloud water or precipitation rate (liter m^{-2} hr^{-1}), mean NO_3^- -N and NH_4^+ -N concentrations in cloud water or precipitation (mg N $liter^{-1}$), air temperature (°C), shortwave radiation (W m^{-2} s^{-1}), wind speed (m s^{-1}) at the top of the canopy, and relative humidity (%) at the top of the canopy were required to drive the model (Figure 5-1). Measurement of driving variables are described in Appendices B and C.

Output variables

Output variables of the model are: (i) amounts of NO_3^- -N and NH_4^+ -N (mg N m^{-2} ground area) retained by each canopy component, and (ii) amounts of solution (liter m^{-2} $event^{-1}$), NO_3^- -N and NH_4^+ -N (mg N m^{-2} $event^{-1}$) in TF on the forest floor (Figure 5-1). Amounts of solution in TF were then converted to depths (mm $event^{-1}$), and NO_3^- -N and NH_4^+ -N were summed to calculate inorganic N fluxes in TF.

Flow functions

Flow functions for solutions (liter m^{-2} hr^{-1}), NO_3^- -N and NH_4^+ -N (mg N m^{-2} hr^{-1}) stored by canopy components are: (i) rates of solution, NO_3^- -N and NH_4^+ -N input in cloud water, precipitation and drainage from other canopy components, (ii) rates of solution output via evaporation (inorganic N mass is conserved), and (iii) rates of drainage of solution, NO_3^- -N and NH_4^+ -N from components (Figures 5-1 and 5-2). Flow functions for the net retention of NO_3^- -N and NH_4^+ -N (mg N m^{-2} hr^{-1}) by canopy components are the net retention rates calculated as a function of the diffusional resistance coefficients and N mass stored in solution by components. Rates of non-intercepted cloud water and precipitation input, and rates of non-intercepted drainage from canopy components are the flow functions for solution (liter m^{-2} hr^{-1}) and NO_3^- -N and NH_4^+ -N (mg N m^{-2} hr^{-1}) in throughfall on the forest floor (Figure 5-1).

Parameter Estimation

Five parameters are necessary for the model: (i) the interception area of epiphytic bryophytes and DOM (EPI1) in canopy Layer 1, (ii) the water storage capacity, S_C, for each canopy component, (iii) diffusional resistance coefficients for net retention of NO_3^- -N and NH_4^+ -N, r_n, for each component, (iv) the drainage coefficient, α, for each component, and (v) the stem drainage parameter for each component.

Interception area of epiphytic bryophytes in canopy Layer 1

The projected surface area (0.5 m^2 m^{-2} ground area) was used for the interception area of epiphytic bryophytes and DOM (EPI1) in canopy Layer 1 for vertically falling precipitation during convective precipitation event simulations. It was not possible to obtain an accurate estimate of the interception area of EPI1 for advective cloud water and precipitation events in the field. Therefore, values of the interception area of EPI1 ranging from 0.5 to 0.9 m^2 m^{-2} were used during initial model development to estimate this parameter for advective event simulations (Table 5-1).

Solution storage capacities of canopy components

Solution storage capacities of canopy components were estimated from literature values (Pócs 1982, Herwitz 1985, Veneklaas et al. 1990), corroborated with results from laboratory leaching experiments with canopy components collected at the field site (Table 5-2). Herwitz (1985) reported that the solution storage capacities of foliage from tropical trees ranged from 0.2 to 0.3 liter $H_2O\ m^{-2}$, consistent with the values obtained for vascular plant foliage at this site. Solution storage capacity values for epiphytic bryophytes and bryophyte, vascular epiphyte and DOM assemblages reported by Pócs (1982), Veneklaas et al. (1990) and from the field site were used in the model (Table 5-2). It was assumed that 50% of the epiphytic component (EPI3) in canopy Layer 3 was composed of bryophytes, vascular epiphytes and DOM, and the remaining 50% was composed of DOM and roots. Solution storage capacity values were multiplied by the appropriate projected surface area (for vascular plant foliage) or appropriate mass (for epiphytic components) to calculate solution storage capacities ($l\ m^{-2}$ ground area) for each component (Table 5-3).

Diffusional resistance coefficients for net retention of inorganic nitrogen

Diffusional resistance coefficients for net NO_3^- -N and NH_4^+ -N retention were estimated from the results of field and laboratory leaching experiments using: (i) vascular plant foliage, (ii) epiphytic bryophytes and DOM, and (iii) assemblages of epiphytic bryophytes, vascular epiphytes and DOM (Chapter 4). In equation (5) derived by Lovett et al. (1989), a fixed value for the diffusional resistance term r_n could be used only when it was assumed that canopy

Table 5-2. Solution storage at saturation (mean ± 1 s.e.) as a percent of dry weight for: (i) epiphytic bryophytes and dead organic matter (DOM), (ii) assemblages of epiphytic bryophytes, vascular epiphytes and DOM, and (iii) DOM and roots only. Sample size is indicated in parentheses where reported. n.d. = not determined.

Location	Solution Storage (mean % of dry wt ± 1 s.e.)		
	Epiphytic Bryophytes and DOM	Assemblages of Epiphytic Bryophytes, Vascular Epiphytes, and DOM	DOM and Roots
Monteverde, Costa Rica[1]	541 ± 47[a] (n=60) to 674 ± 34[b] (n=10)	459 ± 17 (n=18)	285 ± 11 (n=10)
Uluguru Mnts., Tanzania[2]	471	n.d.	n.d.
Santa Rosa de Cabal, Colombia[3]	632 ± 31[c] (n=64)	590 ± 23[d] (n=54)	n.d.

1. K. Clark and N. Nadkarni, unpub. data
2. Pócs 1982
3. Veneklaas et al. 1990

a. Mat, cushion, and turf-forming bryophytes
b. Pendant, fan and tail-forming bryophytes
c. Samples from outer portions of branches
d. Samples from inner portions of branches

Table 5-3. Estimated solution storage capacities (l m^{-2} ground area) of canopy components (from Tables 5-1 and 5-2).

Canopy Layer	Canopy Component	Solution Storage Capacity (l m^{-2})
1	LEAF1	0.75
	EPI1	1.80
2	LEAF2	0.50
	EPI2	2.75
3	LEAF3	0.25
	EPI3	4.20
Sum of Vascular Foliage Layers		1.50
Sum of Epiphyte Layers		8.75
Sum of All Layers		10.25

components stored the same volume of water or were saturated at each time step. However, canopy components store variable amounts of water as they wet up and drain. Therefore, diffusional resistance coefficients were derived to calculate the net retention of NO_3^- -N and NH_4^+ -N as a proportion of the N mass in solution stored by each canopy component at each time step (Table 5-4). During the course of the leaching experiments (Chapter 4), it was assumed that artificial cloud water or precipitation inputs mixed completely with solutions already stored by components, and that components retained NO_3^- -N and NH_4^+ -N from stored solutions only. These assumptions were identical to those made in the model. Net retention of NO_3^- -N and NH_4^+ -N was calculated as a proportion of the N mass in stored solutions, and diffusional resistance coefficients were then derived for each type of component by averaging the proportional retention values from all cloud water and precipitation leaching experiments (Chapter 4, Table 5-4).

Drainage coefficients

The drainage coefficient α in equation (7) was estimated from the results of leaching experiments in the laboratory using: (i) vascular plant foliage, (ii) epiphytic bryophytes and DOM, and (iii) assemblages of epiphytic bryophyte, vascular epiphytes and DOM. Drainage rates, D_t, from components were measured with a tipping bucket rain gage (model #2501, Sierra Misco Environmental Ltd., Victoria, Canada) connected to an automatic data logger

Table 5-4. Diffusional resistance coefficients (r_n) used to calculate net retention of NO_3^- -N and NH_4^+ -N by canopy components.

Canopy Component	Diffusional Resistance Coefficient	
	NO_3^- -N	NH_4^+ -N
Vascular plant foliage (LEAF1,2,3)	20	20
Epiphytic bryophytes and DOM (EPI1)	1.01	1.25
Assemblages of epiphytic bryophytes, vascular epiphytes and DOM (EPI2,3)	1.01	1.25

(Easylogger #EL824-GP, Omidata International, Logan, Utah). The logger was programmed to sum drainage depth at 5 minute intervals.

Analyses of the rates of solution input vs. drainage rates from components indicated that drainage coefficients ranged between ca. 2 and 5, but that they were a non-linear function of water storage by components; drainage coefficients tended to be lower when components were first wetting up, suggesting that they were slightly hydrophobic at that time, and then increased as components approached saturation. To simplify the complexity involved in estimating dynamic values for drainage coefficients, they were assumed to have a fixed value of 5 for all canopy components during all simulations. Sensitivity analysis was performed on values of the drainage coefficient ranging between 1 and 25 for all canopy components simultaneously.

Stem drainage parameter

The amount of drainage from canopy components diverted to stems was not measured at the field site because of logistical difficulty and stemflow was generated at the base of trees only during relatively intense precipitation events. During initial model development, values for the stem drainage parameter ranging from 0.0 to 0.2 (which simulated the diversion of from 0 to 20% of the drainage from each component to stems) were used for all canopy components simultaneously to estimate the value of this parameter.

Model Simulation

The model was written in BASIC programming language. Euler integration was used to solve the flow functions for state variables on a time-step of one hour.

Sensitivity Analyses

To assess the response of the model to selected parameters, sensitivity analyses were performed on values of (i) the interception area of the epiphytic bryophytes and DOM (EPI1) in canopy Layer 1 during advective event simulations, (ii) the diffusional resistance coefficient for net NH_4^+ -N retention, r_n, by all epiphytic components (EPI1, EPI2, EPI3), (iii) the drainage coefficient, α, for all canopy components, and (iv) the stem drainage parameter for all canopy components. One representative event from each of the four event categories was selected for these simulations: (i) cloud water, (ii) mist, (iii) advective precipitation, and (iv) convective precipitation (Appendix B). Meteorological data for the cloud water events were estimated from literature values (Lovett 1984, Mohen and Kadlecek 1989, Miller et al. 1993b), and cloud water chemistry was derived from mean values measured at the field site (Appendix B). Meteorological data and precipitation chemistry for all other events were measured at the field site (Appendices B and C).

Interception area of epiphytic bryophytes in canopy Layer 1

The value of the interception area of epiphytic bryophytes and DOM in EPI1 was altered from 0.5 to 0.9 m^2 m^{-2} ground area. Advective events from each of the three categories were simulated, and TF depth and net retention of inorganic N by the canopy were predicted.

Diffusional resistance coefficient for net retention of ammonium

Values of the diffusional resistance coefficient for the net retention of NH_4^+ -N, r_n, were altered from 1.25 to -1.25 for all epiphytic components (EPI1, EPI2, EPI3) simultaneously. Events from each of the four categories were simulated, and net retention of NH_4^+ -N by the canopy was predicted.

Drainage coefficients

Values of the drainage coefficient α were altered from 1 to 25 for all canopy components simultaneously. Events from each of the four categories were simulated, and TF depth and net retention of inorganic N by the canopy were predicted.

Stem drainage parameter

Values of the stem drainage parameter were altered from 0.0 to 0.2 (simulating from 0 to 20% of drainage from components diverted to stems) for all canopy components simultaneously. Events from each of the four categories were simulated, and TF depth and net retention of inorganic N by the canopy were predicted.

Model Evaluation

To evaluate model performance, the model was simulated using meteorological variables and mean NO_3^- -N and NH_4^+ -N concentrations measured at the field site for three events in each of three categories of precipitation events: (i) mist, (ii) advective precipitation, and (iii) convective precipitation. Criteria used to select these events were that they (i) occurred following at least 48 hours without cloud water or precipitation input, (ii) had complete hourly meteorological data, and (iii) had complete precipitation and TF chemistry. It was necessary to use events that represented initially dry canopy conditions for model evaluation, because this was assumed as an initial condition in the model. Predicted TF depths were compared to mean TF depths measured at the field site, and predicted net retention of inorganic N, NO_3^- -N, and NH_4^+ -N by the canopy was compared to net retention of inorganic N, NO_3^- -N, and NH_4^+ -N estimated from TF measurements at the field site (Appendix C).

Net Retention of Inorganic Nitrogen by Canopy Components

Net retention of inorganic N by individual canopy components was summed at each time step for the three events in each of the four event categories described above. Following an event simulation, net amounts of inorganic N retained were summed for vascular plant foliage (LEAF1, LEAF2, LEAF3) and epiphytic components (EPI1, EPI2, EPI3).

A Wilcoxson Two-sample test was used to evaluate differences in net retention of inorganic N among these two groups. One event from each category was selected to investigate net retention of inorganic N by individual canopy components in detail.

To further investigate the effects of epiphytes on hydrologic and inorganic N fluxes from the atmosphere, reductions of epiphyte mass but not their interception areas were approximated by reducing the solution storage capacities of epiphytic components. Solution storage capacities of epiphytic components (EPI1, EPI2, EPI3) were reduced from between 0% to 90% simultaneously. Throughfall depth and net retention of inorganic N by the canopy were predicted.

Net Retention of Increased Nitrogen Deposition by Canopy Components

The response of canopy components to increased N deposition was explored by increasing NO_3^- -N and NH_4^+ -N concentrations in cloud water and convective precipitation when these two contrasting events were simulated. Concentrations of NO_3^- -N and NH_4^+ -N were increased up to three times ambient levels, and net retention of inorganic N by individual components was predicted. Saturation of the ability of epiphytic bryophytes and DOM (EPI1) in canopy Layer 1 to retain inorganic N was approximated by altering the value of the diffusional resistance coefficient, r_n, for this component from 1.5 to 20. Cloud water and convective precipitation events were simulated with NO_3^- -N and NH_4^+ -N concentrations at three times ambient levels. Net retention of inorganic N by individual canopy components was predicted.

Results and Discussion

Sensitivity Analyses

Interception area of epiphytic bryophytes in canopy Layer 1

Alteration of the value of the interception area of epiphytic bryophytes and DOM (EPI1) in canopy Layer 1 had relatively little effect on predicted TF depths and net retention of inorganic N by the canopy (Figures 5-6 and 5-7). For example, when the interception area of EPI1 was increased from 0.5 to 0.9 m^2 m^{-2} ground area for cloud water event simulations, predicted TF depths changed < 2% and predicted net retention of inorganic N by the canopy changed < 8%.

During initial model development, mean TF depths and inorganic N fluxes in TF at the field site were approximated more closely by the model when 0.9 m^2 m^{-2} was used for the interception area of EPI1 when advective cloud water and precipitation events were simulated. Therefore, this value was used for all subsequent advective event simulations.

Diffusional resistance coefficient for net retention of ammonium

When relatively large positive values of the diffusional resistance coefficient for net retention of

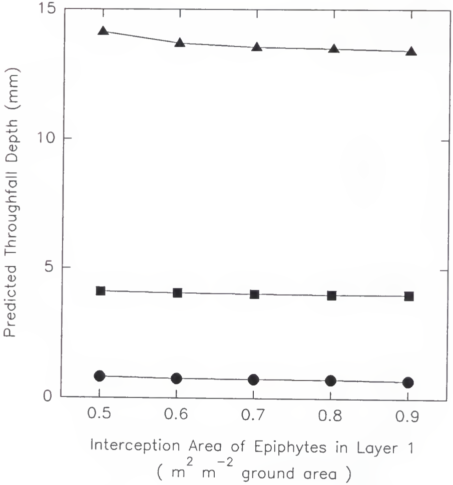

Figure 5-6. Predicted throughfall depth (mm) as of function of the interception area of epiphytic bryophytes and DOM (EPI1) in canopy Layer 1 for cloud water (●), mist (■) and advective precipitation (▲) events.

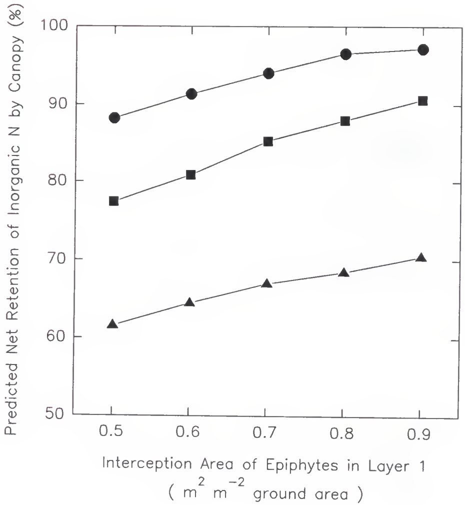

Figure 5-7. Predicted net retention of inorganic N by the canopy (as a percent of inorganic N deposition) as a function of the interception area of epiphytic bryophytes and DOM (EPI1) in canopy Layer 1 for cloud water (●), mist (■) and advective precipitation (▲) events.

NH_4^+ -N by epiphytic components (EPI1, EPI2, EPI3) were used in the model, predicted amounts of NH_4^+ -N retained by the canopy were relatively low (Table 5-5). Small negative values of the diffusional resistance coefficient simulated net NH_4^+ -N leaching from epiphytic components, and net leaching of NH_4^+ -N from the canopy was predicted despite the fact that vascular plant foliage (LEAF2, LEAF3) in the lower canopy retained relatively greater amounts of NH_4^+ -N. Although this is only an approximation of net leaching of NH_4^+ -N from DOM in the canopy, the model predicted net leaching only when relatively high concentrations of NH_4^+ -N occurred in solutions stored by epiphytic components. If model behavior is indicative of conditions in the field, then net leaching of NH_4^+ -N from the canopy observed during intense precipitation event in the early wet season may be due to the leaching of NH_4^+ -N pools produced via episodic or "pulsed" net N mineralization from DOM in the canopy (Clark and Nadkarni 1990, Chapter 6).

Drainage coefficients

Alteration of the values of the drainage coefficient α from 1 to 25 for all canopy components simultaneously had little effect on predicted TF depths and net retention of inorganic N by the canopy.

Stem drainage parameter

Predicted TF depths and predicted net retention of inorganic N by the canopy were both sensitive to the value of the stem drainage parameter (Figures 5-8 and 5-9).

Table 5-5. Predicted net retention of NH_4^+ -N by the canopy as a percent of NH_4^+ -N deposition for simulated cloud water and precipitation events as a function of the diffusional resistance coefficient (r_n) for net retention of NH_4^+ -N by epiphytic components (EPI1, EPI2, EPI3).

Diffusional Resistance Coefficient	Net Retention of NH_4^+ -N (%)			
	Cloud Water	Mist	Advective Precipitation	Convective Precipitation
1.25	96.4	94.9	78.2	38.8
5	92.7	86.7	63.4	30.9
10	89.8	83.3	58.7	29.1
-10	65.8	70.7	45.0	24.9
-5	13.6	59.5	34.9	22.3
-4	-46.0	52.1	28.2	21.0
-3	-271.2	35.7	16.3	18.5
-2	-	-19.4	-20.0	16.2
-1.5	-	-126.8	-80.2	5.0
-1.25	-	-280.9	-156.3	-2.6

Negative values represent net leaching of NH_4^+ -N from the canopy.

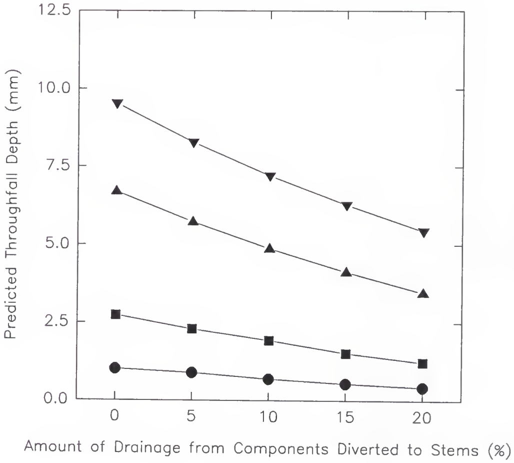

Figure 5-8. Predicted throughfall depth (mm) as a function of the percent of drainage from canopy components diverted to stems for cloud water (●), mist (■), advective precipitation (▲), and convective precipitation (▼) events.

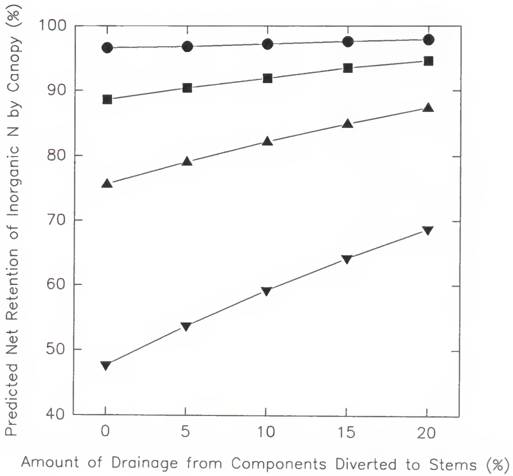

Figure 5-9. Predicted net retention of inorganic N by the canopy (as a percent of inorganic N deposition) as a function of the percent of drainage from canopy components diverted to stems for cloud water (●), mist (■), advective precipitation (▲), and convective precipitation (▼) events.

Alteration of the stem drainage parameter from 0.0 to 0.2 resulted in a ca. 30% reduction in predicted TF depths for all events simulated. Predicted net retention of inorganic N by the canopy increased to greater extent for advective and convective precipitation event simulations when compared to cloud water and mist events over this range of values of the stem drainage parameter, because the precipitation events were characterized by relatively greater solution inputs to, and hence drainage from, all components.

During initial model development, mean TF depths and inorganic N fluxes in TF at the field site were approximated more closely by the model when 0.1 was used for the value of the stem drainage parameter. This value simulated the diversion of 10% of the drainage from canopy components to stems and was used for all subsequent model runs.

Model Evaluation

Hydrologic flux in throughfall

Predicted TF depths were slightly greater for the mist event simulations and consistently less for convective precipitation event simulations when compared to mean TF depths estimated from measurements at the field site (Figure 5-10). Possible explanations for model deviation during mist event simulations include: (i) the model underestimates evaporation from upper portions of the canopy under advective stratus cloud conditions, (ii) greater amounts of solution percolate through epiphyte mats and are diverted to

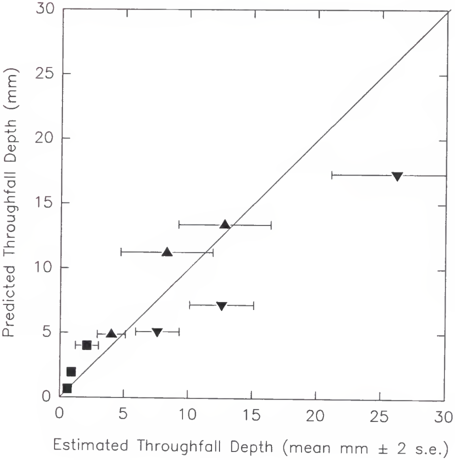

Figure 5-10. Predicted throughfall depth (mm) vs. throughfall depth (mean mm ± 2 s.e., n=20) estimated from field measurements for mist (■), advective precipitation (▲), and convective precipitation (▼) events.

stems than is assumed in the model, (iii) hydrologic flux in TF was underestimated by the sampling network at the field site, and (iv) systematic errors were associated with the measurement of driving variables, particularly relative humidity.

Explanation (i) is likely because recent evidence (e.g., Shuttleworth 1989, Raupach 1989, Calder 1990, Lankreijer et al. 1993) suggests that aerodynamic resistance to momentum r_m may only roughly approximate aerodynamic resistance to evaporation r_a under some atmospheric conditions, and particularly when the canopy is partially or entirely wet. In the model, predicted rates of potential evaporation are a nearly linear function of windspeed, and it is possible that this simplification underestimates the latent heat exchange process during some events. In addition, actual evaporation rates from components are calculated from the the ratio of the amount of solution stored to the solution storage capacity when they are not saturated using equation (3)(Rutter et al. 1971, Gash et al. 1979, Shuttleworth 1988). This may also represent an over-simplification of the resistances to evaporation from canopy components. Eddy correlation techniques would be useful in resolving the uncertainties in estimating evaporation rates from this canopy (Verma et al. 1986, Kelliher et al. 1992, Hollinger et al. 1994).

Explanation (ii) is also likely because twigs and branches in the canopy are covered with continuous mats of epiphytes, and it is possible that relatively large volumes of solution are diverted from the upper canopy to large branches and stems via conduction when rates of precipitation input are low.

Although the relatively high variability in TF depths measured at the field site indicate that drip points occur in this structurally complex forest (cf. Lloyd and Marques 1988, Lloyd et al. 1988, Bruijnzeel 1990, Appendix C), explanation (iii) is unlikely because up to 40 collectors have been used to sample TF at the site and similarly high values for precipitation interception were measured. Explanation (iv) is also unlikely because meteorological data used to drive the model for evaluation simulations were screened carefully, and errors in the measurement of relative humidity and other variables did not exceed 5%.

Predicted TF depths were lower when compared to mean TF depths measured at the field site for the convective event simulations, indicating that the model underestimated hydrologic flux in TF during these simulations (Figure 5-10). All convective events simulated were of relatively short duration (5 to 9 hours) and were characterized by initially high rates of precipitation input to a dry canopy. It is possible that epiphytic components were slightly hydrophobic during the initial stages of these events, similar to their behavior during the initial wetting-up phase during laboratory experiments where the drainage coefficient α was estimated. Since α was assumed to be a fixed value for epiphyte components, initially rapid rates of drainage were likely underestimated in the model, resulting in predicted TF depths that underestimated measured TF depths in the field.

Net retention of inorganic nitrogen by the canopy

When compared to the net retention of inorganic N by the canopy estimated from TF measurements at the field site, the model predicted inorganic N retention by the canopy well (Figure 5-11). In only two cases did predicted values exceed estimated values by two standard errors of the mean. The model slightly underestimated net retention of NO_3^- -N by the canopy for mist and advective precipitation event simulations when compared to values estimated from TF measurements at the field site (Figure 5-12). Since the model slightly overestimated TF depths, it follows that the net retention of NO_3^- -N by the canopy was underestimated for advective event simulations. In addition, although the projected surface area of epiphytic bryophytes in the upper canopy was assumed to be 0.9 m^2 m^{-2} during these simulations, it is possible that the surface area of epiphytic bryophytes is still underestimated. For example, the surface area of epiphylls (bryophytes on vascular plant foliage) in the lower canopy was not accounted for in the model.

The model slightly overestimated net retention of NH_4^+ -N by the canopy for convective precipitation event simulations when compared to estimated values (Figure 5-13).

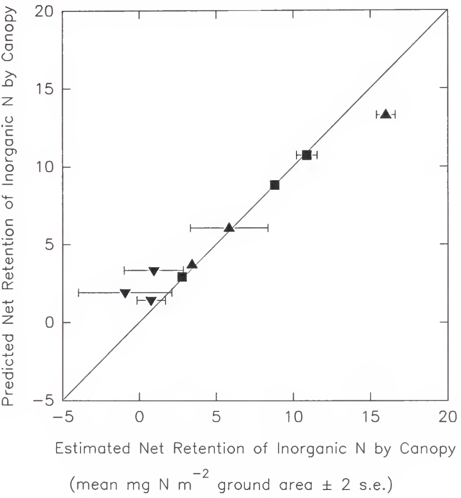

Figure 5-11. Predicted net retention of inorganic N (mg N m^{-2} ground area) by the canopy vs. net retention of inorganic N (mean mg N m^{-2} ground area ± 2 s.e., n=8 to 20) estimated from field measurements for mist (■), advective precipitation (▲), and convective precipitation (▼) events.

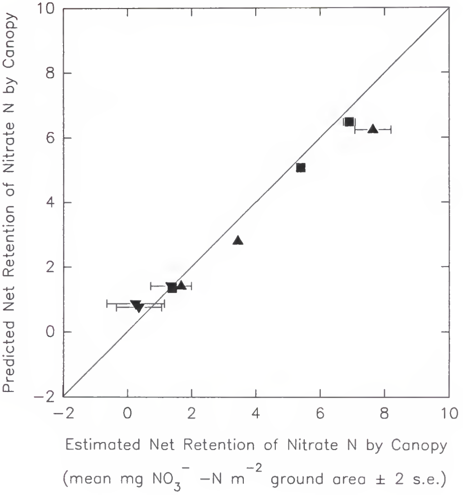

Figure 5-12. Predicted net retention of nitrate -N (mg NO_3^- -N m^{-2} ground area) by the canopy vs. net retention of nitrate -N (mean mg NO_3^- -N m^{-2} ground area ± 2 s.e., n=8 to 20) estimated from field measurements for mist (■), advective precipitation (▲), and convective precipitation (▼) events.

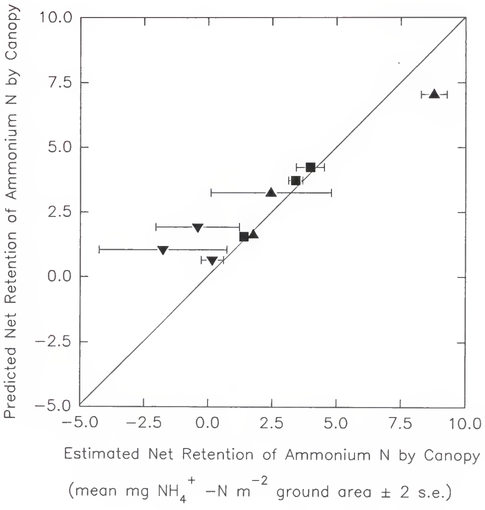

Figure 5-13. Predicted net retention of ammonium -N (mg NH_4^+-N m^{-2} ground area) by the canopy vs. net retention of inorganic N (mean mg NH_4^+ -N m^{-2} ground area ± 2 s.e., n=8 to 20) estimated from field measurements for mist (■), advective precipitation (▲), and convective precipitation (▼) events.

Predicted values for the net retention of NH_4^+ -N may have deviated from estimated values because TF depths were underestimated by the model. In addition, NH_4^+ -N dynamics in DOM were not modelled explicitly. It is likely that pools of NH_4^+ -N in DOM are relatively large early in the wet season (Vance and Nadkarni 1990, Chapter 6), and intense precipitation results in the exchange and net leaching of NH_4^+ -N from these pools.

Overall, predicted values for TF depths and net retention of inorganic N by the canopy approximated those estimated from TF measurements at the field site. Modelling NH_4^+ -N retention by the canopy using a similar approach was also relatively successful for an Abies balsamea canopy (Lovett et al. 1989).

Net Retention of Inorganic Nitrogen by Canopy Components

Predicted net retention of inorganic N by epiphytic bryophytes, vascular epiphytes and DOM was significantly greater than that predicted by vascular plant foliage for all events simulated (Wilcoxson Two-sample test, $P < 0.01$, Table 5-6). Net retention of inorganic N by epiphytic components represented between 61% and 83% of the total predicted net retention of inorganic N by the canopy, and between 33 and 75% of inorganic N deposition to the canopy. Highest net amounts of N retained by epiphytic components were predicted for cloud water and mist event simulations, but vascular plant foliage retained a relatively greater

Table 5-6. Predicted net retention of inorganic N (mg NO_3^- -N + NH_4^+ -N m^{-2} ground area) from cloud water and precipitation by vascular plant foliage and epiphytic components by event category.

Event Category	Net Retention of Inorganic N (mg NO_3^- -N + NH_4^+ -N m^{-2})	
	Vascular Plant Foliage	Epiphytic Components
Cloud Water	1.5	5.3
	2.0	7.4
	3.0	11.2
Mist	0.3	2.3
	1.5	8.2
	2.0	7.1
Advective Precipitation	0.2	2.3
	0.5	5.0
	0.8	10.0
Convective Precipitation	0.1	0.9
	0.1	1.2
	0.1	2.0

proportion of inorganic N during these simulations. These results suggest that epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes and DOM alter inorganic N fluxes substantially as cloud water and precipitation pass through the canopy.

When cloud water and mist events were simulated, predicted amounts of inorganic N retained by components (LEAF1 and EPI1) in canopy Layer 1 were much greater than those predicted for components in canopy Layers 2 and 3 (Figure 5-14). Relatively large amounts of inorganic N retained by components in the upper canopy were likely due to low rates of solution penetration to lower canopy layers when input rates are low, and to low concentrations of inorganic N in solutions reaching components in canopy Layers 2 and 3 because of depletion in the upper canopy. Schaefer et al. (1988) reported similar results for NO_3^- -N and NH_4^+ -N when sampling TF at different depths in a Abies balsamea canopy, as did Lovett et al. (1989) for NH_4^+ -N using a modelling approach for the same canopy.

During simulated advective and convective precipitation events, which were characterized by higher rates of precipitation, components in canopy Layer 1 saturated rapidly, and solution penetration to components in canopy Layers 2 and 3 was relatively greater. Since NO_3^- -N and NH_4^+ -N were depleted only from storage pools on canopy components, relatively greater volumes of solution had minimal interaction with components in the upper canopy,

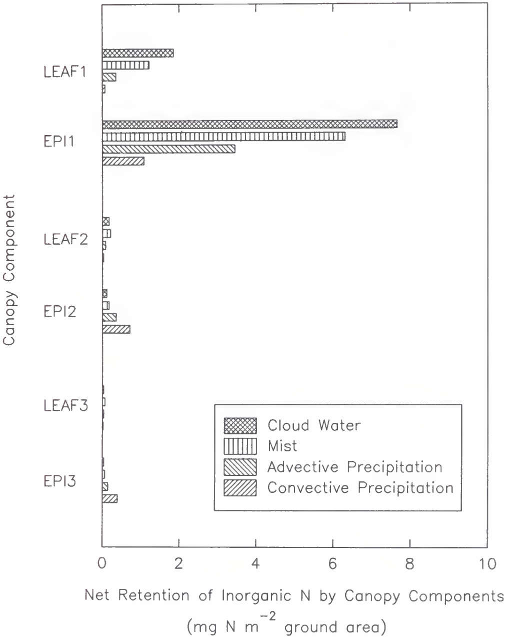

Figure 5-14. Predicted net retention of inorganic N (mg N m^{-2} ground area) by individual canopy components for cloud water, mist, advective precipitation, and convective precipitation events.

and NO_3^- -N and NH_4^+ -N concentrations in solutions reaching components in canopy Layers 2 and 3 reflected those in wet deposition more closely. Epiphytic components in the lower canopy were thus relatively more important in the net retention of inorganic N, while vascular plant foliage in the lower canopy layers again retained relatively little inorganic N.

Reduction of the solution storage capacities of epiphytic components (EPI1, EPI2, EPI3), which simulated a smaller epiphyte mass but did not affect the interception areas of epiphytic components, had a substantial effect on both predicted TF depths and net retention of inorganic N by the canopy for all events simulated (Figures 5-15 and 5-16). For example, when the solution storage capacity of epiphytic components was reduced by 90%, predicted TF depths increased 1.3, 2.1, 4.7, and 6.0 mm for cloud water, mist, advective precipitation and convective precipitation event simulations, respectively. Predicted net retention of inorganic N by the canopy was reduced by 16%, 29%, 46%, and 63% for the same simulations, respectively. Results from these simulations suggest that epiphytes functions as "capacitors" for hydrologic inputs to the canopy (cf. Pócs 1982), and indicate that they are important in the alteration of inorganic N inputs in wet deposition to the canopy.

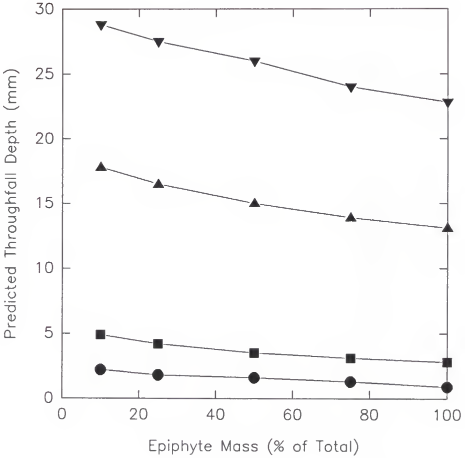

Figure 5-15. Predicted throughfall depth (mm) as a function of the percent of total estimated epiphyte mass in the canopy for cloud water (●), mist (■), advective precipitation (▲), and convective precipitation (▼) events.

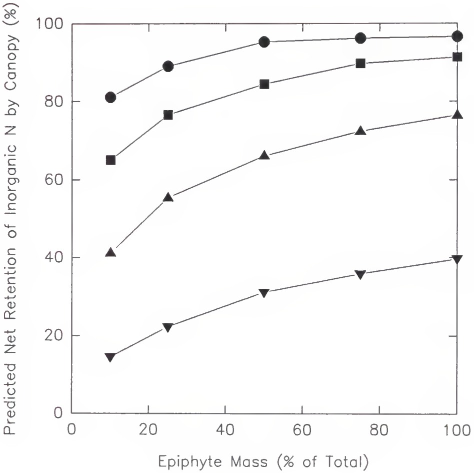

Figure 5-16. Predicted net retention of inorganic N by the canopy (as a percent of inorganic N deposition) as a function of the percent of total epiphyte mass in the canopy for cloud water (●), mist (■), advective precipitation (▲), and convective precipitation (▼) events.

Net Retention of Increased Nitrogen Deposition by Canopy Components

An increase in NO_3^- -N and NH_4^+ -N concentrations from 1 to 3 times ambient levels in cloud water resulted in a nearly linear increase in predicted net retention of inorganic N by all canopy components (Figure 5-17). Components (LEAF1 and EPI1) in canopy Layer 1 again retained the greatest amounts of inorganic N. A nearly linear increase in predicted net retention of inorganic N by components also occurred when concentrations of NO_3^- -N and NH^{4+} -N in convective precipitation were increased from 1 to 3 times ambient levels (Figure 5-18). As in previous convective event simulations, epiphytic components (EPI2, EPI3) in canopy Layers 2 and 3 retained relatively greater amounts of inorganic N when compared to amounts retained during cloud water event simulations.

An increase in the value of the diffusional resistance coefficient for the net retention of NO_3^- -N and NH_4^+ -N from 1.5 to 20 for EPI1 when cloud water events were simulated resulted in a moderate increase in the net retention of inorganic N by components in canopy Layers 2 and 3 (Figure 5-19). Absolute amounts of inorganic N retained by these components were relatively small, but represented up to a 150% increase over the range of diffusional resistance coefficients for EPI1 used for cloud water event simulations. Although absolute amounts of inorganic N retained by epiphytic components (EPI2, EPI3)

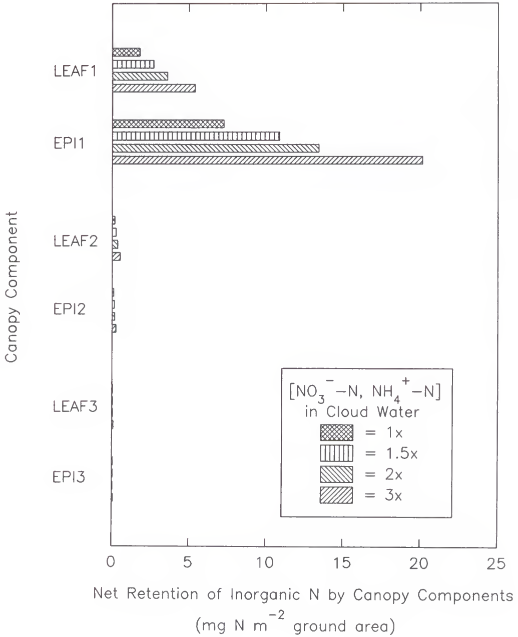

Figure 5-17. Predicted net retention of inorganic N by canopy components for cloud water event simulations where NO_3^- -N and NH_4^+ -N concentrations were increased from 1 to 3 times ambient levels.

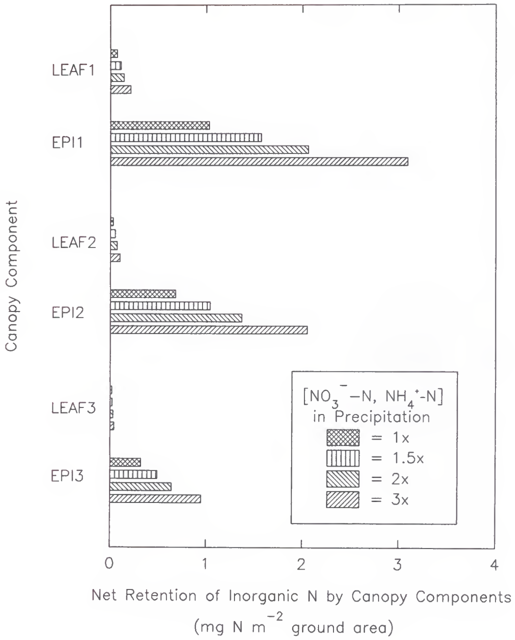

Figure 5-18. Predicted net retention of inorganic N by canopy components for convective precipitation event simulations where NO_3^- -N and NH_4^+ -N concentrations were increased from 1 to 3 times ambient levels.

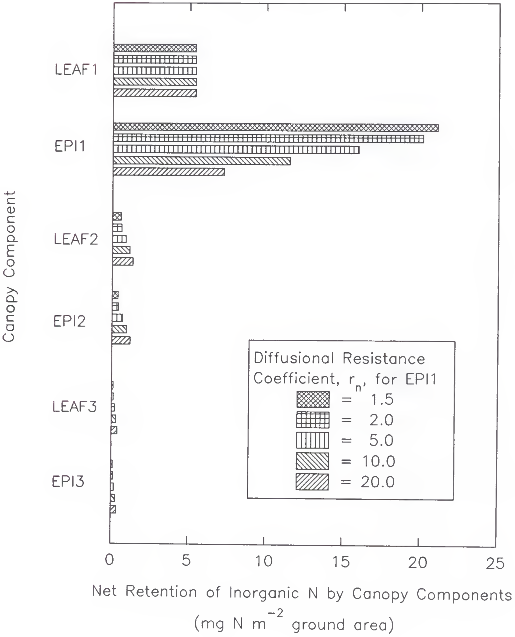

Figure 5-19. Predicted net retention of inorganic N by canopy components for cloud water event simulations using 3 times ambient concentrations of NO_3^- -N and NH_4^+ -N as a function of the diffusional resistance coefficient for EPI1.

in canopy Layers 2 and 3 was greater for the convective event simulations, an increase in the diffusional resistance coefficient for net retention of inorganic N by EPI1 resulted in only a 10% increase in the net retention of inorganic N by these components (Figure 5-20).

Conclusions

Overall, model simulations indicated that epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes, and DOM may play a major role in the alteration of inorganic N inputs in wet deposition to the canopy. Predicted hydrologic and inorganic N fluxes in TF were particularly sensitive to the value of the stem drainage coefficient, which simulated the amount of drainage from components diverted to stems.

The model approximated inorganic N fluxes in TF measured at the field site, thus it also has utility in partitioning the observed net retention of inorganic N by the canopy among epiphytic and vascular plant components: Net retention of inorganic N by the canopy was 0.5 ± 0.1 g N m^{-2} yr^{-1} (mean ± 1 s.e., Appendix C). Predicted net inorganic N retention by epiphytic components was ca. 80% of total net N retention by the canopy for the range of cloud water and precipitation events simulated. Multiplying these values together yields an estimated 0.4 ± 0.1 g N m^{-2} yr^{-1} (mean ± 1 s.e.) retained by epiphytic components, representing ca. 60% of total inorganic N deposition to the

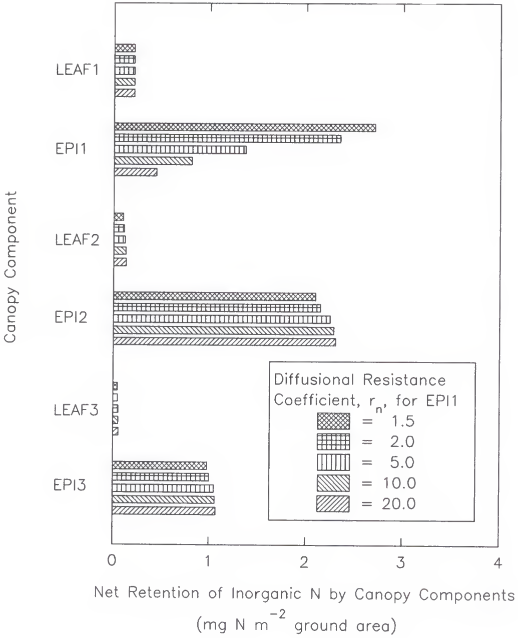

Figure 5-20. Predicted net retention of inorganic N by canopy components for convective precipitation event simulations using 3 times ambient concentrations of NO_3^- -N and NH_4^+ -N as a function of the diffusional resistance coefficient for EPI1.

canopy. These estimates suggest that epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes and DOM play major roles in the regulation of inorganic N fluxes in TF at this site.

Results from the model also indicated that epiphytic bryophytes and DOM in the upper canopy retained a considerable portion of the inorganic N fluxes in cloud water and mist, while inorganic N retention by assemblages of epiphytic bryophytes, vascular epiphytes and DOM was relatively more important during events characterized by higher rates of precipitation. Higher concentrations of inorganic N in cloud water and mist will likely have the greatest effects on components in the upper canopy because relatively little solution percolates to lower canopy layers and inorganic N is relatively depleted in these solutions. In contrast, higher concentrations of inorganic N in precipitation may affect all epiphytic components, but apparently has little effect on vascular plant foliage, assuming that diffusional resistance coefficients remain unchanged. In terms of the amounts of inorganic N retained by epiphytic components in the lower canopy layers, increased inorganic N concentrations in cloud water and precipitation are apparently more important than saturation of the ability of epiphytic bryophytes in the upper canopy to retain inorganic N. The implications of these results are discussed in greater detail in Chapter 7.

CHAPTER 6
DECOMPOSITION, NITROGEN DYNAMICS, AND INORGANIC NITROGEN TRANSFORMATIONS IN EPIPHYTIC BRYOPHYTE LITTER

Introduction

Tropical montane cloud forests (TMCF) are characterized by large accumulations of litter, humus and soil organic matter (SOM), representing the major pools of carbon (C) and nitrogen (N) in these ecosystems (Jenny et al. 1949, Edwards and Grubb 1977, Grieve et al. 1990, Bruijnzeel and Proctor 1993). Despite these large pools of N, relatively low rates of litter decomposition (Edwards 1977, LaCaro and Rudd 1985, Nadkarni and Matelson 1992b) and net N mineralization from SOM (Marrs et al. 1988, Vitousek et al. 1988, Vance and Nadkarni 1990) have led a number of investigators to conclude that N availability in TMCF is low when compared to tropical forests at lower elevations. Mineralization of N from these pools by microbial populations, along with N deposition from the atmosphere and N_2 fixation, control rates of N cycling and thus N availability, potentially limiting the productivity of these forests (Grubb 1977, Edwards and Grubb 1982, Vitousek and Sanford 1986, Tanner et al. 1990, 1992).

Dead organic matter (DOM) also accumulates on stems and branches in the canopy of TMCF. Estimates of mass and N storage in canopy DOM range up to 2800 g m^{-2} and 40 g N m^{-2} ground area, respectively, and represent up to two times forest floor mass (Edwards and Grubb 1977, Nadkarni 1984, Vance and Nadkarni 1990, Nadkarni and Matelson 1992a, Hofstede et al. 1993, Table 1-1). Since litterfall inputs from host trees to the epiphyte community are apparently minor (< 1% of fine litterfall flux to the forest floor at this site; Nadkarni and Matelson 1991), canopy DOM is likely derived primarily from epiphytic vegetation. A substantial portion of canopy DOM may be derived from epiphytic bryophytes because they accumulate mass in the canopy (Chapter 3), and may be characterized by relatively low rates of litter decomposition (Berg 1984, Van Toreen 1988, Rochefort et al. 1990, Longton 1992).

Canopy DOM represents a continuum of decomposition products from recently formed litter to highly decomposed humus (sensu Melillo et al. 1989). Vance and Nadkarni (1990) reported relatively low rates of net N mineralization from canopy humus when compared to SOM at this site, suggesting that N availability in the canopy is also limited. In contrast, rates of N leaching and net N mineralization from recently formed litter of epiphytic bryophytes may be considerable when compared to those characterizing canopy humus (Coxson 1991). Relatively high rates of N leaching and net N mineralization have also been reported from litter of terrestrial bryophytes when compared to more highly decomposed peat (e.g., Clymo and Hayward 1982, Brock and Bregman 1989, Verhoeven et al. 1990). Therefore, N leaching and net N mineralization from litter derived from epiphytic bryophytes may represent important processes controlling N availability in the canopy.

The epiphyte community in TMCF is characterized by highly diverse and moderately productive assemblages of vascular epiphytes and hemi-epiphytes (Gentry and Dodson 1987, Benzing 1990, Ingram and Nadkarni 1993), many of which are apparently unable to retain N directly from wet deposition (Chapter 4). Vascular epiphyte roots are associated with bryophyte litter throughout the canopy (Ter Steege and Cornelissen 1989, Ingram and Nadkarni 1993), and root biomass in accumulations of canopy humus on larger branchens is similar to an equivalent volume of soil on the forest floor (Vance and Nadkarni 1992), suggesting that N transfer from DOM to vascular epiphytes may be substantial. However, few studies exist to evaluate the role of DOM derived from epiphytic bryophytes in the C dynamics and N cycle of TMCF. The objectives of this investigation were to characterize (i) the rates of decomposition of litter derived from epiphytic bryophytes in the canopy and on the forest floor, (ii) the N dynamics of litter in the canopy, (iii) the inorganic N pools in litter and humus in the canopy, and (iv) the rates of net N mineralization from litter and humus in the canopy of a TMCF.

Methods and Materials

Litterbags in the Canopy

Litter samples from common life-forms of epiphytic bryophytes (pendants, fans, tails, mats, wefts, turfs and cushions; life-form terminology sensu Mägdefrau 1982, During 1992) were collected from the canopy and recent treefalls at the site in July and August 1991. Older and recently dead shoots with > 90% of the foliage intact were separated by removing live, green shoots and more highly decomposed litter and humus, and then pooled to produce a homogeneous mixture. One hundred litterbags (ca. 10 x 15 cm, 2 mm mesh size) were weighed and a subsample (ca. 8-12 g wet weight) of litter was loosely packed into each litterbag. Litterbags were dried at 60 °C for 48 to 72 hours to prevent growth of live shoots (Berg 1984, Van Toreen 1988, Rochefort et al. 1990) and weighed again. Subsamples of the fresh litter mixture were ground and stored in clean glass vials until tissue N concentrations were analyzed.

Eight dominant trees with moderate to heavy epiphyte loads were selected for the study, proportionally representing the most frequently occurring species in the canopy in the 4 ha study plot (Table 6-1). Middle to upper locations in the canopy were accessed using modified rock climbing techniques. Litterbags were placed on branches of various sizes and inclinations beneath: (i) actively-growing bryophyte shoots, (ii) accumulated bryophyte litter, and

Table 6-1. Trees used for the canopy litterbag and field nitrogen mineralization studies: "L" indicates placement of litterbags, "RC" indicates placement of ion exchange resin cores.

Species	DBH (cm)	Activity
Ficus tuerckheimii	238.0	RC
Ficus tuerckheimii	192.0	L
Ficus tuerckheimii	185.0	L, RC
Meliosma ideopoda	95.5	L
Meliosma ideopoda	72.5	L, RC
Ocotea tonduzii	124.0	L, RC
Ocotea tonduzii	99.0	L
Ocotea tonduzii	72.5	L
Pouteria viride	70.5	L

(iii) vascular epiphytes but above humus accumulations. Twelve to 24 litterbags were placed in each tree. Two or three litterbags were collected from each tree at 3, 6, 9, 12, 15 and 24 months. Litterbags were taken to the laboratory and air dried immediately following harvest. Vascular plant roots and any extraneous material were removed from litterbag samples, and bryophyte litter and roots were dried separately at 60 °C for 48 hours and then weighed. A subsample of litter from each litterbag was ground and stored in clean glass vials until tissue N concentrations were analyzed.

Litterbags on the Forest Floor

Fifty litterbags of epiphytic bryophyte litter were prepared following the protocol above. Five 100 m^2 plots were located randomly on the forest floor within the 4 ha study area. Ten litterbags were placed at random locations within each sub-plot. Two litterbags were harvested from each plot at 3, 6, 9, 12 and 15 months, and were treated in an identical manner as the canopy litterbags following collection.

Inorganic Nitrogen Pools in Litter and Humus

Litter samples from selected epiphytic bryophyte life-forms (fans, tails, mats, wefts and turfs) were collected at the site and fresh litter was separated following the protocol above. Samples were separated into sets consisting of two subsamples (ca. 1 g equivalent dry weight). One subsample was placed in a washed (0.1 M HCl) and rinsed (deionized (DI-) water) 250 ml polypropylene bottle containing 100 ml DI-water, and the other subsample was placed in a washed and rinsed polypropylene bottle containing 2 M KCl. Bottles were shaken for 1 hr at 150 rpm, then extracted for an additional 23 hr. Solutions were decanted, filtered (0.45 μm GF/A Gelman filters) and stored at 4 °C until analyzed (< 1 week). Litter samples were recovered from the bottles, dried at 60 °C for 48 hours and weighed.

Fresh litter from pendant bryophytes, litter from litterbags that had been in the canopy for two years, and canopy humus were extracted in 2 M KCl. Samples of pendant bryophytes were collected from the canopies of three trees, and fresh litter was selected following the protocol above. Litterbag and humus samples were collected from the canopies of three trees and roots were removed. Samples were extracted, filtered, stored and weighed following the protocol describe above.

Net Nitrogen Mineralization from Litter and Humus

Ion exchange resin cores (DiStefano and Gholz 1986) were used to estimate rates of net N mineralization from fresh litter from a mixture of bryophyte life-forms, 2-year-old litter from litterbags and canopy humus. Samples were collected and separated following the protocol above and further separated into sets consisting of 2 subsamples (ca. 1.0 g equivalent dry weight for litter, ca. 4.0 g equivalent dry weight for humus). One subsample was placed on top of a pair of cation and anion ion exchange resin rings (0.5 cm tall, 7 cm diameter, containing ca. 5 g Dowex 50W-X8, 20-50 mesh size cation exchange resin beads, ca. 5 g Ionac NA-38, 16-50 mesh size anion exchange resin beads) in an open-ended PVC cylinder (12 cm tall, 7 cm inner diameter) that had been washed (0.1 M HCl) and rinsed (DI-water). A second pair of cation and anion resin rings was placed above the sample in the cylinder to absorb ions entering in throughfall. The other sub-sample was immediately extracted in 100 ml of 2 M KCl following the protocol described above.

Resin cores were stored in the dark in the laboratory at 18 to 23 °C and leached with DI-water every 2 days (equivalent to 1.0 cm day^{-1}), or placed in mid-canopy locations of three trees at the field site (Table 6-1). Resin cores were harvested after 21 days. Bryophyte litter and humus samples were extracted in 2 M KCl, dried and weighed following the protocol described above. Extraneous material was removed from anion and cation resin rings and they were extracted separately in 100 ml of 2 M KCL following the same protocol for litter samples.

Chemical Analyses

Tissue N concentrations and inorganic N concentrations in extracts were analyzed using standard procedures (Appendix A).

Data Analyses

Cumulative mass and N losses from epiphytic bryophyte litterbags were calculated as a percent of initial sample mass and N content. Inorganic pools in litter and humus samples were expressed on a g dry weight basis. Net NH_4^+ -N and NO_3^- -N mineralization was calculated as ((μg NH_4^+ -N or NO_3^- -N extracted from resin rings + μg NH_4^+ -N or NO_3^- -N extracted from samples in cylinders after 21 days) g dry wt^{-1}) - ((μg NH_4^+ -N or NO_3^- -N) g dry wt^{-1}) extracted from subsamples at the beginning of the experiment (DiStefano and Gholz 1986).

T-tests were used to detect differences in (i) cumulative mass loss from epiphytic bryophyte litterbags among locations within sampling dates, (ii) first-year mass loss from epiphytic bryophyte litterbags in the canopy when compared to estimated first-year mass loss from fine vascular plant litter in the canopy (30% mass loss; Nadkarni and Matelson 1991), (iii) first-year mass loss from epiphytic bryophyte litterbags on the forest floor when compared to estimated first-year mass loss from fine vascular plant litter on the forest floor (ca. 60% mass loss; Nadkarni and Matelson 1992b), (iv) N concentrations in epiphytic bryophyte litter in the canopy when compared to initial N concentrations in litter within sampling dates, and (v) levels of inorganic N extracted from fresh litter among extractants. One-way ANOVAs were used to detect differences in (i) levels of extractable inorganic N among types of DOM, (ii) rates of net N mineralization from fresh litter among sampling times, and (iii) rates of net N mineralization among types of DOM. Paired sample T-tests were used to contrast NO_3^- -N vs. NH_4^+ -N for all extractions and net N mineralization experiments. Homogeneity of group variances was determined with Bartlett's test, and data were log-transformed and retested where necessary. SYSTAT (Wilkinson 1987) statistical packages were used for all analyses.

Results

Mass Loss from Litter

Cumulative mass loss from epiphytic bryophyte litterbags in the canopy was 17% after one year and 19% after two years (Table 6-2). Cumulative mass loss from epiphytic bryophyte litterbags on the forest floor was 29% after one year. Cumulative mass losses from litterbags on the forest floor were greater than those from litterbags in the canopy for most sampling dates (T-tests, $P < 0.01$) (Table 6-2). First-year mass loss from epiphytic bryophyte litterbags in the canopy was different when compared to mass

Table 6-2. Cumulative mass loss (mean % ± 1 s.e.) as a percent of initial mass from epiphytic bryophyte litter in litterbags in the canopy and on the forest floor.

Month	Mass loss (mean % ± 1 s.e.)	
	Canopy	Forest Floor
3	7.9 ± 1.8^a (16)	19.2 ± 1.5^b (10)
6	14.6 ± 1.4^a (17)	23.9 ± 2.4^b (10)
9	15.0 ± 1.9 (19)	23.4 ± 3.0 (7)
12	17.3 ± 1.5^a (17)	29.1 ± 2.2^b (7)
15	18.5 ± 4.0^a (13)	32.7 ± 2.7^b (9)
24	19.3 ± 2.3 (17)	n.d.

Different superscripts indicate significant differences in mass loss among locations within months (T-tests, $P < 0.01$).
Sample size is indicated in parentheses.
n.d. = not determined.

loss from vascular plant litter in the canopy (T-test, $T_{16} = 1.99$, $P < 0.07$). First-year mass loss from epiphytic bryophyte litterbags on the forest floor was also less when compared to the estimated mass loss from fine vascular plant litter on the forest floor (T-test, $T_6 = 4.966$, $P < 0.01$).

Nitrogen Dynamics in Litter

The initial N concentration of epiphytic bryophyte litter was 12.7 ± 0.4 mg N g^{-1} (mean ± 1 s.e., n=4). Nitrogen concentrations in litterbags decreased to 67% of this value after one year in the canopy (Table 6-3). Percent N mass remaining in litterbags was ca. 55% of the initial N mass after one year. Net N immobilization may have occurred between 12 and 15 months, but percent N mass was only ca. 68% of the initial N mass after 15 months.

Inorganic Nitrogen Pools in Litter and Humus

Inorganic N extracted from fresh litter from the mixture of bryophyte life-forms was dominated by NH_4^+ -N for both the DI-water and 2 M KCl extractions, and represented > 95% of the extracted inorganic N (paired-sample T-tests, $P < 0.05$) (Table 6-4). Greater amounts of NH_4^+ -N but not NO_3^- -N were extracted from litter with 2 M KCl when compared to DI-water extractions (T-test, $P < 0.01$), indicating the presence of an exchangeable pool of NH_4^+ in bryophyte litter.

Table 6-3. Nitrogen concentrations (mean mg N (g dry wt)$^{-1}$ ± 1 s.e.) and percent of initial nitrogen mass remaining (mean % ± 1 s.e.) in litterbags containing epiphytic bryophytes. Mean nitrogen concentration in litter at t=0 was 12.7 ± 0.4 mg N (g dry wt)$^{-1}$ (mean ± 1 s.e., n=4).

Months in Canopy	N Concentration mg N (g dry wt)$^{-1}$	Percent N Remaining
3	9.0 ± 1.1^{a} (7)	66.3 ± 8.8
6	9.2 ± 0.5^{a} (9)	61.5 ± 3.5
9	8.5 ± 0.6^{a} (8)	56.5 ± 3.6
12	8.5 ± 0.5^{a} (9)	54.9 ± 3.1
15	10.2 ± 1.0 (9)	67.5 ± 6.3
24	8.5§ (8)	62%

Superscripts indicate significant differences from t=0 values (T-tests, $P < 0.05$).
Sample size is indicated in parentheses.
§. Samples bulked for analysis.

Table 6-4. Inorganic nitrogen (mean μg N $(g\ dry\ wt)^{-1} \pm 1$ s.e.) extracted from fresh litter of mixed bryophyte life-forms with either de-ionized water or 2 M KCl.

Extractant	Extractable N μg N $(g\ dry\ wt)^{-1} \pm 1$ s.d.		
	NH_4^+ -N	NO_3^- -N	Inorganic N
DI-water (n=5)	48.7 ± 2.5^a	2.2 ± 0.3	50.9 ± 2.7^a
2 M KCl (n=5)	87.4 ± 2.7^b	2.3 ± 0.3	89.7 ± 3.0^b

Sample size is indicated in parentheses.
Different superscripts indicate significant differences among extractants (T-tests, $P < 0.01$).

Differences were detected in 2 M KCl extractable inorganic N among fresh pendant litter, fresh mixed litter, 2-year-old litter, and humus (ANOVA, $F = 5.299$, $P < 0.05$) (Table 6-5). Inorganic N pools were largest in pendant bryophyte litter and smallest in humus. Amounts of extractable NH_4^+ -N were greater than NO_3^- -N for all sample types, and represented > 60% of extractable inorganic N (Paired-sample T-tests, $P < 0.001$). Nitrate -N pools were greatest in 2-year-old litter (Table 6-5).

Net Nitrogen Mineralization from Litter and Humus

Rates of net N mineralization from fresh litter from mixtures of bryophyte life-forms were different among sampling periods (ANOVA, $F = 10.882$, $P < 0.01$) (Table 6-6). Net NH_4^+ -N mineralization was greater than net nitrification during all three periods (Paired-sample T-tests, $P < 0.001$), and represented > 70% of net N mineralization, although increased nitrification was detected in the November 1992 field experiment (Table 6-6).

Net N mineralization was greater from fresh and 2-year-old litter than from humus (ANOVA, $P < 0.05$)(Table 6-7). Rates of net NH_4^+ -N mineralization were greater than net nitrification for fresh litter and 2-year-old litter, but not for humus (Paired- Sample T-tests, $P < 0.01$). Net NH_4^+ -N mineralization represented ca. 90% of total net N mineralization from fresh and 2-year-old litter (Table 6-7).

Table 6-5. Inorganic nitrogen (mean μg N (g dry wt)$^{-1}$ ± 1 s.e.) extracted from various litter types and canopy humus with 2 M KCl.

Sample Type	Extractable N μg N (g dry wt)$^{-1}$ ± 1 s.e.		
	NH_4^+ -N	NO_3^- -N	Inorganic N
Pendant Litter (n=5)	545.8 ± 24.2^a	4.2 ± 0.4^a	550.0 ± 24.5^a
Mixed Litter (n=9)	96.2 ± 5.0^b	15.4 ± 7.9^a	111.6 ± 11.6^b
2-year-old Litter (n=3)	85.5 ± 13.3^b	52.8 ± 3.8^b	138.3 ± 16.7^b
Canopy Humus (n=3)	73.2 ± 6.6^b	0.4 ± 0.1^c	73.5 ± 3.3^c

Sample size is indicated in parentheses.
Different superscripts indicate significant differences among sample types (ANOVA, $P < 0.05$).

Table 6-6. Net nitrogen (mean μg N (g dry wt)$^{-1}$ day^{-1} ± 1 s.e) mineralization from fresh litter of mixed bryophyte life-forms measured in ion exchange resin cores.

Date	Location	Net N Mineralization μg N (g dry wt)$^{-1}$ day^{-1}		
		NH_4^+ -N	NO_3^- -N	Inorganic N
Oct '91 (n=5)	Lab.	12.4 ± 1.6	0.5 ± 0.2^a	12.8 ± 1.7^{ab}
Nov '92 (n=5)	Field	11.8 ± 1.4	4.6 ± 0.9^b	16.3 ± 1.6^a
Aug '93 (n=5)	Field	8.3 ± 0.9	0.7 ± 0.3^a	9.1 ± 0.8^b

Sample size is indicated in parentheses.
Superscripts indicate significant differences among dates (ANOVA, $F_{2,12} = 15.010$, $P < 0.01$ for NO_3^- N mineralization and $F_{2,12} = 10.882$, $P < 0.01$ for inorganic N mineralization).

Table 6-7. Net nitrogen (mean μg N (g dry wt)$^{-1}$ day^{-1} ± 1 s.e) mineralization from fresh bryophyte litter, 2-year-old bryophyte litter from litterbags and canopy humus measured in ion exchange resin cores during August 1993.

Sample Type	Net N Mineralization μg N (g dry wt)$^{-1}$ day^{-1}		
	NH_4^+ -N	NO_3^- -N	Inorganic N
Recent Litter (n=5)	8.3 ± 0.9^a	0.7 ± 0.3	9.1 ± 0.8^a
2-year-old Litter (n=5)	7.1 ± 1.8^a	0.8 ± 0.5	7.9 ± 1.9^a
Canopy Humus (n=5)	0.9 ± 0.3^b	bdl	0.9 ± 0.3^b

Sample size is indicated in parentheses.
Superscripts indicate significant differences among sample types (ANOVA, $F_{2,12}$ = 11.394, $P < 0.01$ for net NH_4^+ -N mineralization and $F_{2,12}$ = 16.422, $P < 0.01$ for net inorganic N mineralization).
bdl = below detection limits.

Discussion

Mass Loss from Litter

Mass loss from litter is an integration of litter comminution, leaching of soluble compounds and particles, and gaseous losses of CO_2 and H_20 due to microbial respiration. Mesh size of litterbags potentially influences mass loss due to exclusion of macrofauna and the leaching of particles, but has little effect on microbial populations. The mesh size of litterbags used here was larger than those used in terrestrial bryophyte litterbag studies (2 mm mesh size vs. 0.2 to 1 mm mesh size; Rosswall et al. 1975, Berg 1984, Van Toreen 1988, Rochefort et al. 1990, Johnson and Damman 1991), which may have affected the loss of particles. However, litterbags in the canopy were placed below live epiphytes and accumulated litter at the beginning of the experiment, and litterbags on the forest floor were incorporated into the litter layer relatively rapidly, presumably reducing losses of particulates. Heat pretreatment of bryophyte litter may have also affected rates of mass loss (Berg 1984, Van Toreen 1988, Rochefort et al. 1990).

Despite these methodological limitations, first-year mass loss values for canopy and forest floor litterbags were within and slightly greater than the range of first-year mass loss values (4% to 28%) reported for terrestrial bryophyte litterbags in other studies (Table 6-8). Mass

Table 6-8. Cumulative mass loss (% of initial mass) from bryophyte litter in litterbags.

Location	Genus	Cumulative Mass Loss (% of initial mass)		
		1 yr	2 yr	3 yr
Monteverde, Costa Rica[a]				
Canopy	Mixed	17	19	-
Forest floor	Mixed	29	-	-
Scots Pine, Sweden[b]	Dicranum	15	26	34
South Limburg, Netherlands[c]	Calliergonella	18 to 28	18 to 40	-
Palsa Mire, N. Sweden[d]	Sphagnum	4 to 7	8 to 19	-
Ontario, Canada[e]	Sphagnum	5 to 27	16 to 24	14 to 27
Moor House, UK[f]	Sphagnum	6 to 18	-	-
Akhult Mire, S. Sweden[g]	Sphagnum	11 to 22	13 to 28	-
Scots Pine, Sweden[h]	Sphagnum	27	33	-

a. This study
b. Berg 1984
c. Van Tooren 1988, values reported from 2 sites.
d. Rosswall et al. 1975
e. Rochefort et al. 1990; after 14, 26, and 38 months
f. Clymo 1965
g. Johnson and Damman 1991; after 10 and 22 months
h. Berg 1984

Values for Sphagnum are for acrotelm (aerobic) sites only. Ranges are given for mean mass loss of different species of Sphagnum (where reported).

loss from canopy litterbags decreased to ca. 2% during the second year, within the range of second-year mass loss values (1% to 5%) reported from other studies. Initially high rates of mass loss from litter are typically a result of the utilization of more labile C fractions (e.g., soluble cellular constituents and cellulose) by microbial populations. Lower rates of mass loss during the second year indicated that the remaining litter was composed of more recalcitrant C fractions (Berg and Staff 1981, Melillo et al. 1982, Berg 1984, Melillo et al. 1989).

Concomitant with the decomposition of bryophyte litter is a compaction of the litter structure, resulting in an increase in bulk density (Johnson et al. 1990, Malmer and Wallen 1993). The amorphous humified material on remaining leaf and stem tissue in litterbags in the canopy was similar in appearance to native canopy humus, suggesting that epiphytic bryophytes are a major contributor to the accumulated humus in the canopy (Edwards and Grubb 1977, Nadkarni 1984, Vance and Nadkarni 1990).

Differences in the rates of mass loss from bryophyte litter among locations were likely due to differences in both abiotic and biotic conditions. For example, the canopy is characterized by prolonged dry periods and rapid drainage when compared to the forest floor, which potentially limits microbial and fungal activity in the canopy. Therefore, microclimate apparently exerts an effect on rates of litter decomposition (Zak et al. 1993, Hogg et al. 1994). Dead organic matter in the canopy is more acidic than the forest floor (Vance and Nadkarni 1990, Hofstede et al. 1993), also potentially affecting microbial and fungal populations. In addition, a relatively lower abundance of some macrofaunal groups has been reported in the canopy when compared to the forest floor (Nadkarni and Longino 1990).

When compared to fine vascular plant litter at the same site, the relatively low rates of decomposition reported for bryophyte litter indicate that litter quality also exerts a major effect on the decomposition process. Bryophyte litter contains relatively high concentrations of lignin-like compounds (Berg 1984, Chapin et al. 1987) and polymerized aliphatic compounds (Kälviäninen et al. 1985) which are recalcitrant with respect to microbial degradation (Melillo et al. 1982, Berg 1984, Longton 1992). Consequently, litter derived from epiphytic bryophytes is disproportionately important in C accumulation in the canopy and on the forest floor. Investigations concerning the functioning of bryophytes in terrestrial ecosystems have arrived at similar conclusions (Berg 1984, Oechel and Van Cleve 1986, Longton 1992, Malmer and Wallen 1993).

Nitrogen Dynamics in Litter

Nitrogen dynamics during the decomposition of vascular plant litter have been characterized as a 3-phase process (i) initial N leaching, (ii) net N immobilization, and (iii) final net N release (Berg and Staff 1981, Mellilo et al.

1982). In contrast, the mean N mass of epiphytic bryophyte litter decreased to 55% of initial N mass after one year and apparently remained at < 65% after two years. Results suggested that (i) labile C fractions were utilized or leached rapidly, (ii) labile N fractions were leached and mineralized rapidly, and (iii) net N immobilization by microbial populations was minimal. Limited net N immobilization is also supported by comparing net N mineralization rates from fresh and 2-year-old litter, for which rates were not significantly different. The remaining N mass in litter was apparently recalcitrant, and was likely associated with structural C fractions (Brock and Bregman 1989). These results are consistent with the patterns of N dynamics reported for terrestrial bryophyte litter (Berg 1984, Van Toreen 1988, Brock and Bregman 1989).

Inorganic Nitrogen Pools in Litter and Humus

Differences in the amounts of NH_4^+ -N extracted with DI-water and 2 M KCl suggest that cation exchange sites on cell walls mediate the storage and release of NH_4^+ -N from bryophyte litter (Clymo and Hayward 1982, Richter and Dainty 1989a). In contrast, relatively smaller pools of KCl exchangeable NO_3^- -N in litter are likely a result of much lower anion exchange site densities on cell walls (Richter and Dainty 1989b), and potentially lower rates of nitrification in the canopy.

Inorganic N pools in fresh pendant bryophyte litter were much greater than those reported for Sphagnum litter, but N pools were only slightly greater in fresh mixed and 2-year-old litter (Verhoeven et al. 1990)(Table 6-9). Inorganic N pools were dominated by NH_4^+ -N for all litter types, consistent with results reported for canopy humus (Vance and Nadkarni 1990, Hofstede et al. 1993) and terrestrial bryophyte litter (Urban and Eisenreich 1988, Verhoeven et al. 1990). Extractable NO_3^- -N pools were more variable and may have reflected high spatial variability of nitrifying bacteria populations in the canopy.

Inorganic N pools in humus were similar to values reported for DOM samples during the wet season by Vance and Nadkarni (1990), and greater than their values obtained during other times of the year (Table 6-9). Values were greater than those reported for Sphagnum peat at 25 cm depth by Verhoeven et al. (1990), and considerably greater than those reported by Rosswall and Granhall (1980) for peat samples from a sub-arctic mire.

Net Nitrogen Mineralization from Litter and Humus

Rates of net N mineralization from fresh and 2-year-old litter were slightly greater than those reported for Sphagnum litter (Verhoeven et al. 1990) (Table 6-10). Net N mineralization rates from canopy humus reported here were similar to previously reported rates for this site (Vance and Nadkarni 1990), and similar to those reported for peat

Table 6-9. Nitrogen contents (mg N g^{-1}) and extractable inorganic N (μg N g^{-1}) in bryophyte litter, canopy humus, and Sphagnum litter.

Sample Type	N content (mg N g^{-1})	Extractable Inorganic N (μg N g^{-1})	
		NH_4^+ -N	NO_3^- -N
Epiphytic Bryophyte Litter[a]			
Fresh Litter	12.7	96.2 (15.0)	15.4 (7.9)
2-year-old Litter	8.5	85.5 (13.3)	52.8 (3.8)
Canopy Humus[b]	21.6	21.1 to 64.8 (8.2) (8.6)	0.6 to 3.8 (0.5) (0.3)
Sphagnum Litter[c]			
10 cm Depth	6.9 to 18.1	33 to 72 (6) (12)	bdl
25 cm Depth	6.9 to 18.1	30 to 38 (6) (9)	bdl

a. This Study.
b. Vance and Nadkarni 1990; range of mean values during different seasons.
c. Verhoeven et al. 1990; range of mean values from ombrotrophic bogs in the Netherlands.
Values are means, s.e. in parentheses where reported.
bdl = below detection limits.

Table 6-10. Net N mineralization (μg N (g dry wt)$^{-1}$ day^{-1}) from bryophyte litter, canopy humus, and Sphagnum litter.

Sample Type	Net N Mineralization Rate (μg N (g dry wt)$^{-1}$ day^{-1})		
	NH_4^+ -N	NO_3^- -N	Inorganic N
Epiphytic Bryophyte Litter[a]			
Fresh Litter	8.3 to 12.4 (0.9) (1.6)	0.5 to 4.6 (0.2) (0.9)	9.1 to 16.3 (0.8) (1.6)
2-year-old Litter	7.1 (1.8)	0.8 (0.5)	7.9 (1.9)
Canopy Humus[b]	n.r.	-0.4 to 0.1 (0.0) (0.1)	-1.1 to 3.6 (0.7) (1.0)
Sphagnum Litter[c]			
10 cm Depth	0.7 to 6.5 (0.7) (1.3)	bdl	2.7 to 6.5 (0.7) (1.3)
25 cm Depth	0.5 to 2.6 (0.2) (0.7)	bdl	0.5 to 2.6 (0.2) (0.7)

a. This Study; range of mean values during different experiments.
b. Vance and Nadkarni 1990; range of mean values during different seasons.
c. Verhoeven et al. 1990; range of mean values from ombrotrophic bogs in the Netherlands.
Standard errors are in parentheses.
n.r. = not reported.
bdl = below detection limits.

from a sub-arctic mire (0.4 to 0.6 μg N g^{-1} day^{-1}; Rosswall and Granhall 1980).

Initially high rates of inorganic N release from litter are a result of cellular leaching from labile N pools and mineralization by microbial populations, coupled with apparently low rates of net N immobilization. Net NH_4^+ mineralization leads to an increase in NH_4^+ pools on cell wall exchange sites, and subsequent leaching or exchange releases NH_4^+ to canopy solutions. As decomposition progresses and labile C and N pools in litter are depleted, rates of leaching and mineralization are presumably reduced and approach the relatively low rates characterizing canopy humus.

Verhoeven et al. (1990) suggested that the availability of labile C limits microbial communities in Sphagnum litter, subsequently limiting net N immobilization. Vance and Nadkarni (1990) reported a significant increase in CO_2 evolution and a decrease in levels of extractable inorganic N following the addition of labile C (as glucose) to samples of canopy humus, consistent with the hypothesis of Verhoeven et al. (1990). In contrast, Damman (1988) suggested that microbial activity in peat is limited by phosphorus (P) supply rather than labile C. Hogg et al. (1994) have reported a trend towards greater CO_2 evolution from Sphagnum litter with higher N and P concentrations from a range of bogs in Sweden, but their results are not inconsistent with the hypothesis of Verhoeven et al. (1990) because N and P in fresh litter are likely associated with labile C compounds.

Overall, these results suggest that the decomposition rate of epiphytic bryophyte litter is relatively slow when compared to that of vascular plant litter at this site. In contrast, the rate of net N mineralization from recently formed bryophyte litter is relatively high when compared to canopy humus, suggesting that potentially rapid rates of N cycling occur in microsites in the canopy. Although we lack information on the mass of epiphytic bryophyte litter in the canopy, it is instructive to compare the amounts of net N release from recent litter, 2-year-old litter and from canopy humus. In this exercise, net accumulation of bryophyte litter in the canopy was calculated by subtracting an estimate of annual bryophyte litterfall to the forest floor (35 g m^2 yr^{-1}; Nadkarni and Matelson 1992a) from a range of annual production estimates (46 to 74 g m^{-2} yr^{-1}, Chapter 3). Assuming that epiphytic bryophyte biomass is in steady state, it is estimated that 9 to 32 g m^{-2} yr^{-1} of bryophyte litter accumulates in the canopy annually. Mean net N mineralization rates from litter and humus reported here and by Vance and Nadkarni (1990), and DOM mass estimates in the canopy (Table 1-1) were then used to calculate annual net N mineralization from litter vs. humus in the canopy. It was assumed that mean rates were representative of net N mineralization rates in the canopy during the wet and transition seasons (8 months), and that rates were minimal during the dry season (4 months). Estimated net N mineralization from recent to 2-year-old litter was 0.04 to 0.1 g N m^{-2} yr^{-1}, and that from canopy humus 0.7 g N m^{-2} yr^{-1}. Although the estimated mass of recently formed to 2-year-old litter is ca. 1 to 2% of the total mass of DOM in the canopy, these calculations show that net N mineralization from bryophyte litter represented from 6 to 14% of the N mineralized from canopy humus.

Although these estimates are only approximate, they suggest that litter derived from epiphytic bryophytes may be important in N cycling in the canopy despite the relatively low rate of decomposition. Redistribution of N from litter to new shoots has been reported for terrestrial bryophytes (Malmer and Holm 1984, Malmer 1988, Urban and Eisenreich 1988, Rydin and Clymo 1989, Bates 1992). In addition, root biomass is relatively large in the canopy (Vance and Nadkarni 1992), and fine root ingrowth was detected in canopy litterbags (ca. 0.03 g roots (g dry wt $litter^{-1}$) yr^{-1}). Inorganic N in throughfall was 0.2 g N m^2 yr^{-1}, and represented < 25% of the estimated inorganic N mineralized in the canopy, suggesting that epiphytic bryophytes and vascular epiphytes exerted a strong control over N released from litter and humus. Episodes of NH_4^+ leaching from the canopy were detected only at the beginning of the wet season (Clark and Nadkarni 1990). Flushes of N mineralization following rewetting have been noted in a range of soils (Cambell et al. 1988, Cabrera 1993) and from epiphyte assemblages exposed to intense precipitation (Coxson 1991). It is possible that initially high rates of NH_4^+ mineralization in the canopy are decoupled from biotic demand at the onset of the wet season, potentially due to differential effects of prolonged dry periods on epiphytic bryophytes, vascular epiphytes and microbial populations. Although we have little information on the kinetics of N mineralization rates from litter and humus, biotic demand likely increases as the wet season progresses, resulting in reduced leaching losses from the canopy.

It is likely that atmospheric deposition and N_2-fixation are the ultimate sources of N for epiphytic vegetation in TMCF (Benzing 1990, Frahm 1990b, Nadkarni and Matelson 1991), but the results presented here suggest that the internal cycling of N in litter and humus approaches these sources in magnitude. The relative importance of N sources for epiphytes may have a strong seasonality; internal cycling of N is probably more important in the wet season when N concentrations in precipitation are low and net N mineralization rates are relatively high. The kinetics and seasonality of inorganic N transformations in litter and humus, as well as N uptake by vascular epiphytes, hemiepiphytes, and assimilation by host tree roots, require further investigation before internal N cycling in the canopy of TMCF can be adequately characterizied.

CHAPTER 7
SYNTHESIS, IMPLICATIONS, AND CONCLUSIONS

Net Accumulation and Cycling of Nitrogen by Epiphytic Bryophytes

Epiphytic bryophytes accumulated N via net uptake in new growth (Chapter 3) and bryophyte-derived litter was characterized by relatively low rates of decomposition and N loss (Chapter 6). Net accumulation of N by epiphytic bryophytes in the canopy was calculated by subtracting the rate of N loss from bryophyte-derived litter from the rate of N accumulation by epiphytic bryophytes in the canopy, and net accumulation of N on the forest floor was calculated by subtracting the rate of N loss from litter from the litterfall N flux in epiphytic bryophytes. Resultant rates were 0.1 to 0.4 g N m^{-2} yr^{-1} in the canopy and 0.3 g N m^{-2} yr^{-1} on the forest floor (Table 7-1).

Results further indicated that epiphytic bryophytes and DOM regulated some of the N fluxes in this ecosystem, suggesting that they played roles in controlling rates of N cycling and therefore N availability in the canopy. A portion of the N accumulated by epiphytic bryophytes in new growth was retained from atmospheric deposition (Chapter 4), and net retention of inorganic N by epiphytic bryophytes and epiphytes assemblages consisting of epiphytic bryophytes,

Table 7-1. Accumulation and net accumulation of N (g N m^{-2} yr^{-1}) by epiphytic bryophytes, and other selected N fluxes measured or estimated at the field site.

Process	Nitrogen Flux (g N m^{-2} yr^{-1})	
	Canopy	Forest Floor
Accumulation by Epiphytic Bryophytes[a]	0.7 to 1.1	-
Epiphytic Bryophyte Litterfall[b]	-	0.5
N Leaching, Net N Mineralization[c]	0.1 to 0.2	0.2
Net Accumulation by Epiphytic Bryophytes	0.1 to 0.4	0.3
Atmospheric Deposition[d,e]	0.7	-
Throughfall[d,e]	-	0.2
Net Retention by Canopy[d,e]	0.5	-
Net Retention by Epiphytes[e,f]	0.4	-
N_2-Fixation[g]	0.6 to 1.0	-
Litterfall[b]		
Total Fine	-	10.1
Epiphytes	-	0.8

a. Chapter 3
b. Nadkarni and Matelson 1992a
c. Calculated from N dynamics in litter; Chapter 6
d. Appendix C
e. Inorganic N only
f. Chapter 5
g. D. Schaefer, unpub. manuscript

vascular epiphytes, and DOM represented ca. 60% of total inorganic N deposition to the canopy (Chapter 5, Table 7-1). Following shoot mortality, a portion of the N in recently formed litter was potentially cycled rapidly via N leaching and net mineralization of primarily NH_4^+ -N while the remaining N was relatively recalcitrant (Chapter 6). Therefore, epiphytic bryophytes and DOM regulated N inputs from the atmosphere and rates of N transformations in the canopy, suggesting that they played important roles in controlling rates of N cycling and N availability in the canopy at this site (Table 7-1).

Although it is premature to calculate definitive C and N budgets for the epiphyte community due to inadequate estimates of NPP of vascular epiphytes and uncertainties concerning pathways and rates of internal N cycling in the canopy, it is of value to compare the rates of N accumulation and net N accumulation by epiphytic bryophytes to other ecosystem level fluxes of N at this site (Table 7-1). Accumulation and net accumulation of N by epiphytic bryophytes represent a major portion of the N inputs in atmospheric deposition and newly-fixed N, but represent only 7 to 11% and 4 to 7% of the annual flux of N in fine litterfall to the forest floor, respectively. Therefore, although rates of N accumulation and net N accumulation by epiphytic bryophytes and DOM are relatively small when compared to the annual litterfall flux of N, these components are disproportionately important in the net accumulation of N from allochthonous (primarily atmospheric) sources in this ecosystem (Table 7-1).

Other research at this site has indicated that the shoots of epiphytic bryophytes are an important location for N_2-fixation by free living cyanobacteria, and fixation rates were estimated to range from 0.6 to 1.0 g N m^{-2} yr^{-1} (D. Schaefer, pers. com.). Epiphytic bryophytes and DOM may have also regulated rates of N_2-fixation in the canopy, because it is likely that soluble C compounds leached from these components contributed to the C requirements of cyanobacteria (Coxson et al. 1992). A portion of the newly fixed N may have been assimilated by epiphytic bryophytes (cf. Alexander et al. 1978, Bentley and Carpenter 1984, Bentley 1987), or assimilated following excretion by invertebrates grazing on cyanobacteria (Jones and Wilson 1978).

Epiphytic Bryophytes and Increased Nitrogen Deposition

Epiphytic bryophytes retained inorganic N from atmospheric deposition efficiently (Chapter 4, 5), thus they may be one of the first ecosystem components affected by increased N deposition to TMCF. Effects of chronic, long-term N additions to epiphytic bryophytes and the epiphytic community are currently unknown. However, increased N deposition to TMCF ecosystems is likely to have a number of effects, including: (i) initial stimulation of NPP of epiphytic bryophytes, (ii) increased N concentrations in epiphytic bryophytes and DOM, and (iii) increased rates of N leaching and net mineralization of N from DOM.

Where increased N deposition is not associated with appreciable increases in the acidity, O_3 and other pollutants (Warneck 1988, Andreae et al. 1988, Crutzen and Andreae 1990, Keller et al. 1991, Johnson and Lindberg 1992), a "fertilizer effect" is likely to occur and may initially stimulate NPP of epiphytic bryophytes. Interactions among increased N deposition, increased phosphorus (P) deposition due to biomass burning (Lewis 1981, K. Clark, unpub. data) and gradual increases in atmospheric CO_2 levels may further stimulate NPP of epiphytic bryophytes (Proctor 1982, Aro et al. 1984, Sveinbjornsson and Oechel 1992, Jauhiainen et al. 1994).

Increased N deposition may also lead to higher N concentrations and higher N to P ratios in epiphytic bryophyte tissue. Although a higher rate of NPP effectively "dilutes" N concentrations in tissue (Malmer and Holm 1984, Malmer 1990, Aerts et al. 1992), other constraints on bryophyte growth (e.g., light levels, plant water status, P limitation) will likely result in greater concentrations of N in epiphytic bryophyte tissues. Relatively high tissue N concentrations have been noted for epiphytic bryophytes (Farmer et al. 1991) and terrestrial bryophytes (Ferguson et al. 1984, Malmer 1988, Pitcairn et al. 1991, Aerts et al. 1992, Baddeley et al. 1994) from temperate ecosystems characterized by high rates of N deposition from the atmosphere (Chapter 3).

Rates of N leaching and net mineralization of N from litter derived from epiphytic bryophytes may increase as a function of tissue N concentrations. Larger pools of NH_4^+ -N on exchange sites and net NH_4^+ -N release from litter potentially leads to increased rates of N cycling and, therefore, increased N availability in the canopy. Decomposition and herbivory rates may also be stimulated by higher tissue N concentrations, further increasing N availability in the canopy (cf. Clymo and Hayward 1982, Lee and Studholme 1992). Although rates of N_2-fixation by cyanobacteria in the canopy may be affected by higher N concentrations in bryophyte shoots, litter and canopy solutions, experimental evidence for a negative feedback mechanism on N_2-fixation rates is lacking.

Increased rates of N cycling and greater N availability in the canopy have considerable implications for the conservation of biotic diversity in the canopy of TMCF. Although little is known concerning the N requirements and N limitation of vascular epiphytes in situ, a number of taxa have been characterized by a relatively low capacity for ion assimilation (e.g., Orchidaceae; Benzing 1989, 1990, Hew et al. 1993). If N supply limits the NPP of certain taxa more than others, changes in floristic composition and community structure are probable. Increased N deposition and increased rates of N cycling in the canopy will tend to favor species that have a greater capacity to alter growth rates as a result of changes in N availability (cf. Chapin 1980). Relatively high rates of N deposition have led to significant changes in the floristics and community structure of terrestrial and aquatic ecosystems (Heil and Diemont 1983, Bobbink 1991, Morris 1991, Marrs 1993, Sutton et al. 1993, Baddeley et al. 1994).

It is plausible that chronic, long-term increased N deposition to TMCF may alter the epiphyte community from a system characterized by high species diversity, relatively low rates of NPP, high rates of inorganic N retention from the atmosphere, and low rates of internal N cycling to a more dynamic system characterized by lower species diversity, higher rates of NPP, lower rates of inorganic N retention from the atmosphere, and greater rates of internal N cycling. Appreciable changes in NPP of epiphytic vegetation also has implications for stand dynamics, because larger accumulations of epiphytes may increase rates of branch and treefalls. Although experimental evidence for the effects of increased N deposition to epiphytic communities is lacking, chronic N additions have apparently affected terrestrial ecosystems in a similar manner (McNulty and Aber 1993).

The concept of "critical loads" for N deposition is well-defined (cf. Schulze et al. 1989, Aber 1992, Rosen et al. 1992, Stevens et al. 1994), but characterization of these levels for specific ecosystems is difficult

(Stevens et al. 1994, De Vries et al. 1994). It is probable that the epiphyte community will be affected by increased N deposition before symptoms are detected in other components of TMCF ecosystems. Long-term increased N deposition to TMCF will likely have to be substantial before N saturation (sensu Aber et al. 1989, Johnson 1992) and NO_3^- leaching from below the rooting zone occurs (Johnson et al. 1991, Johnson and Lindberg 1992, Stevens et al. 1994), although some effects have been noted in temperate montane forests after relatively small additions in the supply of N (McNulty and Aber 1993, Stevens et al. 1994). Nitrification rates in soils from TMCF are relatively low when compared to those characterizing tropical lowland forests (Tanner 1977, Marrs et al. 1988, Vitousek et al. 1988, Vance and Nadkarni 1990), and SOM may be a major sink for inorganic N additions, at least in the short term (e.g., Johnson 1992, Tanner et al. 1992). In addition, evidence suggests that tree growth is N limited in some TMCF, suggesting that additional N inputs to the forest floor may be immobilized by plant uptake (Tanner 1977, Tanner et al. 1990, 1992). However, because epiphytic components are very effective at retaining N from atmospheric deposition, the potential effects of increased N deposition to this extremely diverse community must be addressed if we are to establish realistic "critical loads" for N in TMCF.

Conclusions

1. Epiphytic bryophytes accumulated N in new growth (Chapter 3). Although they represent relatively minor pools of C and N in the canopy (ca. 5% of total estimated mass at the field site; Table 1-1), epiphytic bryophytes are a highly dynamic component of this ecosystem. Net production of epiphytic bryophytes was estimated at 46 to 74 g m^{-2} yr^{-1}, and N accumulation in new growth was estimated at 0.7 to 1.1 g N m^{-2} yr^{-1}. Previous research at this site has indicated that epiphytic bryophytes contributed 5% (35 g m^{-2} yr^{-1}) of the mass and 7% (0.6 g N m^{-2} yr^{-1}) of the N in fine litterfall inputs to the forest floor (Nadkarni and Matelson 1992a). Net production of epiphytic bryophytes exceeded the estimated rate of bryophyte litterfall to the forest floor, but differences were not significant due in part to the high variability in NPP estimates. However, results suggested that epiphytic bryophytes accumulated 11 to 39 g mass m^{-2} yr^{-1} and 0.1 to 0.5 g N m^{-2} yr^{-1} in the canopy.

2. Litter derived from epiphytic bryophytes decomposed slowly relative to fine vascular plant litter both in the canopy and on the forest floor (Chapter 6). Mean cumulative mass loss from epiphytic bryophyte litterbags was 17% after 1 year and 19% after 2 years in the canopy, and 29% after 1 year on the forest floor. The N dynamics of litter indicated that ca. 60% of the initial N mass remained after 2 years in the canopy. Consequently, epiphytic bryophytes were disproportionately important in

the net accumulation of mass and N both in the canopy and on the forest floor of this ecosystem.

3. A portion of the N accumulated by epiphytic bryophytes was retained from atmospheric deposition (Chapters 4, 5). Results from the leaching experiments using epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes, and DOM indicated that these components retain inorganic N from solutions when relatively steep concentration gradients form across foliar surfaces. Both components retained > 80% of the inorganic N additions in artificial cloud water and mist solutions. Deionized water rinses following exposure to solutions failed to leach NO_3^- from epiphytic bryophytes, suggesting that retained NO_3^- had been assimilated. Net leaching of NH_4^+ was more substantial but not significant following exposure to relatively N-depleted solutions, and was likely due to exchange from cell wall sites or leaching of accumulated litter. In contrast to the patterns of N retention observed for these epiphytic components, vascular plant foliage had little effect on inorganic N additions in cloud water and mist solutions. Results suggested that the presence of a thick, waxy cuticle on foliar surfaces resulted in considerable diffusional resistance to net inorganic N retention.

4. Retention of inorganic N from atmospheric deposition by epiphytic bryophytes and epiphyte assemblages altered inorganic N fluxes to the forest floor (Chapter 5).

Results from the canopy hydrology and N flux model suggested that epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes, and DOM altered inorganic N inputs in wet deposition as solutions passed through the canopy. When a range of cloud water and precipitation events was simulated and mean inorganic N fluxes in throughfall at the site were approximated, the model predicted that epiphytic bryophytes and epiphyte assemblages retained from 60% to 85% of the total inorganic N retained by the canopy. The model also predicted that epiphytic bryophytes and DOM in the upper canopy would retain a relatively large proportion of the total net N retention by the canopy during cloud water and mist events. When epiphyte mass in the canopy was progressively reduced in the model, increased hydrologic and inorganic N fluxes to the forest floor were predicted, further suggesting that epiphytic components play an important role in the alteration of inorganic N inputs in wet deposition to the canopy.

Total deposition of inorganic N to the canopy was estimated at 0.7 g N m^{-2} yr^{-1} and estimated net retention of inorganic N by the canopy was 0.5 g N m^{-2} yr^{-1} (Appendix C). When predictions from the canopy hydrology and N flux model were compared to these values, results suggested that epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes and DOM retained 0.4 g N m^{-2} yr^{-1}, representing ca. 60% of total inorganic N deposition to the canopy. Nitrate flux to the forest floor was < 20% of that in atmospheric deposition to the canopy, and leaching experiments and model predictions suggested that epiphyte bryophytes retained the majority of the NO_3^- in wet deposition to the canopy. As a result, although we know little concerning the retention of NO_3^- by fine roots and microbial populations on forest floor or of NO_3^- leaching from the forest floor, it is likely that NO_3^- retention by epiphytic bryophytes reduces leaching losses of NO_3^- from this site.

5. In contrast to the relatively slow rates of mass loss from epiphytic bryophyte litter, rates of N leaching and net N mineralization were initially substantial from recently formed bryophyte litter in the canopy (Chapter 6). Results suggested that rates of net N mineralization from recently formed bryophyte litter were greater than those characterizing more highly decomposed canopy humus. Results further suggested that considerable N cycling in recently formed litter may occur in the canopy, primarily as NH_4^+ -N. Ingrowth of fine roots from vascular epiphytes into epiphytic bryophyte litterbags was ca. 0.02 g (g dry wt litter^{-1}) yr^{-1}, thus mineralized N from recently formed litter is likely to be important in the N supply to both living bryophyte shoots and vascular epiphytes. The remaining N in litter is apparently recalcitrant and cycles slowly in litter and humus, and eventually falls to the

forest floor (Nadkarni and Matelson 1992a, Hofstede et al. 1993).

Epiphytic bryophytes presumably play similar roles in the net accumulation and cycling of N in other TMCFs. Although inputs of N from the atmosphere have been calculated to exceed net N uptake in woody biomass increment in some TMCF (Weaver et al. 1986, Bruijnzeel 1990, Bruijnzeel et al., 1993), the few estimates for leaching losses of N suggest that they were relatively low, or net ecosystem accumulation of N was reported (Lugo 1986, King and Yang 1984, Cheng et al. 1987, cited in Bruijnzeel 1990). It is clear that we need more information to (i) construct C and N budgets for the canopy, (ii) evaluate the role of epiphytic bryophytes and other biotic components in regulating leaching losses of N from TMCF, and (iii) estimate "critical loads" of N for TMCF ecosystems.

APPENDIX A
CHEMICAL ANALYSES

Tissue Nitrogen

Epiphytic bryophyte tissue samples and pine foliage standards (Forest Response Program quality assurance samples #02 and #31) were dried at 60 °C for 24 to 48 hours. Subsamples (ca. 0.1000 g) were placed in 75 ml digestion tubes and 2 ml of concentrated sulfuric acid was added to each tube. Digestion tubes were placed on a Technicon BD 40 block digester that had been preheated to 340 °C. Digestion tubes were removed from the block after 30 minutes, allowed to cool, and 1-2 drops of hydrogen peroxide were added to each tube. Digestion tubes were replaced on the block for 15 to 20 minutes. This procedure was repeated (2 to 3 times) until digests were clear. Digestion tubes were then allowed to cool and digests were brought up to 25 ml volume with deionized water. Sulfuric acid blanks and diluted ammonium standards (0.1 M NH_4Cl; Orion 951006) were also digested. Nitrogen concentrations in digests were analyzed as NH_4^+ -N in duplicate using the protocol described below following neutralization and dilution with low-N NaOH and EDTA.

Nitrate and Ammonium in Solutions and Extracts

Nitrate + nitrite (NO_2^-) concentrations in solutions and KCl extracts were determined using a sulfanilamide-napthylethylene-diamine colorimetric technique following NO_3^- reduction with a cadmium column (Mackereth et al. 1978, Page et al. 1982). Deionized water or 2 M KCl blanks and two standards (0.14 and 0.56 mg NO_3^- -N l^{-1}; diluted in matrix matched solutions using volumetric glassware from 0.1 M $NaNO_3$ standards; Orion #920706) were analyzed in quadruplicate sets with samples. Samples which exceeded this range were diluted appropriately and re-analyzed. Ammonium concentrations were determined using an indophenol blue colorimetric technique (Harwood and Kuhn 1970, Page et al. 1982). Deionized water or 2 M KCl blanks and three standards (0.47, 0.93 and 1.4 mg NH_4^+ -N l^{-1}; diluted in matrix matched solutions using volumetric glassware from 0.1 M NH_4Cl standards; Orion #951006) were analyzed in quadruplicate sets with samples. Samples which exceeded this range were diluted appropriately and re-analyzed. All colorimetric analyses were performed on a Sequoia Turner 340 or a Spectrometric 501 colorimeter equipped with a semi-automated flowcell assembly.

Ions in Cloud Water, Precipitation, and Throughfall

Within 24 hours of collection, pH was determined on unfiltered subsamples using a Corning model 120 pH meter calibrated with Fisher pH 4.00 and pH 7.00 standards.

Subsamples were then filtered with deionized water-rinsed Gelman AE 0.45 μm pore size filters and stored at 4 °C until analyzed. Filtered subsamples were analyzed for NH_4^+ and NO_3^- + NO_2^- within 2 weeks of collection for most (>90%) samples. Sodium (Na^+), magnesium (Mg^{2+}), calcium (Ca^{2+}), and potassium (K^+) were determined using standard procedures on a Varian Model AA6 Atomic Absorption Spectrophotometer at the Marine Sciences Institute Analytical Laboratory, University of California, Santa Barbara, or on a Perkin Elmer Model 603 AAS at the Analytical Research Laboratory, University of Florida. Deionized water was analyzed as blanks, and Fisher Scientific 0.1 M reference solutions were diluted appropriately and analyzed as standards. An air-acetylene flame was used for all analyses, and lanthanum additions at approximately 500 mg l^{-1} were used to reduce interferences during Mg^{2+} and Ca^{2+} analyses.

APPENDIX B
CLOUD WATER AND PRECIPITATION CHEMISTRY AT A TROPICAL MONTANE CLOUD FOREST SITE

Introduction

Cloud water and precipitation chemistry at temperate montane cloud forest sites has been the focus of considerable research over the last decade (e.g., Lovett et al. 1982, Dollard et al. 1983, Fowler et al. 1988, Weathers et al. 1988, Mohnen and Kadlecek 1989, Johnson and Lindberg 1992). These investigations have indicated that the concentrations of major ions in cloud water are typically three to ten times greater than those in precipitation, and that anthropogenic emissions of NO_x and SO_2 have clearly increased concentrations of NO_3^-, SO_4^{2-} and H^+ in cloud water and precipitation. Rates of ion deposition to montane forests are partially a function of cloud exposure (Lovett and Kinsman 1990, Vong et al. 1991), and, as a result, ion deposition is typically greater to montane cloud forests when compared to forests at lower elevations (Crossley et al. 1992, Johnson and Lindberg 1992, Miller et al. 1993a). The potential for forest decline, N saturation and acidification of soils, and relatively high concentrations of NO_3^- and H^+ in surface waters has prompted concern for the effects of increased ion deposition to these ecosystems

(Schulze 1989, Aber 1992, Johnson and Lindberg 1992, Stevens et al. 1994).

Less information is available for cloud water and precipitation chemistry at tropical montane cloud forest (TMCF) sites (Asbury et al. 1988, Weathers et al. 1988, Veneklaas 1990, McDowell and Asbury 1993). However, increased combustion of biomass and fossil fuels, and changes in land use practices have led to an increase in the emissions of nitric oxide (NO) and ammonia (NH_3) at tropical latitudes (Talbot et al. 1988, Galloway 1989, Crutzen and Andreae 1990, Keller et al. 1991, Galloway et al. 1994). Reports from lowland sites have indicated regional effects of biomass burning on bulk precipitation chemistry (Lewis 1981, Kellman et al. 1982, Hendry et al. 1984) and, more recently, on air chemistry (Crutzen et al. 1985, Delaney et al. 1985, Andreae et al. 1988a, 1990, Artaxo et al. 1988, 1990). Conversion of forests to pasture and croplands may also lead to increased emissions of NO and NH_3, particularly where N fertilizers are used (Harper et al. 1983, Whitehead and Raistric 1990, Sanhueza et al. 1990, Davidson et al. 1991, Hutchinson and Brams 1992, Keller et al. 1993). These activities potentially lead to greater concentrations of inorganic N and H^+ in cloud water and precipitation in TMCF, but few measurements have been reported. The objective of this study was to characterize the concentrations of NO_3^-, NH_4^+, H^+ and other major ions in cloud water and precipitation at a TMCF site.

Methods and Materials

Site Description

Research was conducted at two sites in the Monteverde Cloud Forest Reserve (MVCFR). In addition to the previously described leeward cloud forest site (LCF), samples were also collected at a windward cloud forest site (WCF; Lawton and Dryer 1980) located on the continental divide ca. 1.2 km east-northeast of the LCF site. Elevation at the WCF site is 1460 m. Immersion in a hill cap cloud occurs more frequently at the WCF site, facilitating the collection of cloud water samples.

Definition of Events

Cloud water and precipitation events were delimited by at least 12 hours without measurable cloud water or precipitation. Samples collected during non-precipitating cloud immersion events, where visibility was reduced to < 0.5 km and there were zero to trace amounts of deposition to a standard rainfall gage, are defined here as representing "cloud water" (Table B-1). Samples collected during precipitating cloud immersion events at sustained windspeeds > 2 m s^{-1} are defined as "mist". Precipitation samples characterized by minimal cloud immersion at sustained windspeeds > 2 m s^{-1} are defined as "advective precipitation". Precipitation samples collected from cumulus or stratocumulus cloud with sustained windspeeds generally

Table B-1. Meteorological conditions, collector type, number of events, and number of samples or subsamples collected at the WCF and LCF sites.

	Cloud Water or Precipitation Category			
	Cloud Water	Mist	Advective	Convective
Wind speed ($m\ s^{-1}$)	> 2	> 2	> 2	< 2
Cloud Immersion	Yes	Yes	No	No
Precipitation	No	Yes	Yes	Yes
Collector type	ASRC cloud collector	ASRC cloud collector	ASRC cloud collector	Bulk precip.
Location	WCF	WCF,LCF	WCF,LCF	LCF
Duration of Sampling Period (hr)	1 to 12	1 to 72	1 to 72	24 to 72
Number of Events	15	32	54	68
Number of Samples or Sub-Samples	34	44	76	47

Sampling dates for the WCF site: 15 Apr 88 to 15 May 88[a], 31 Dec 90 to 6 Jan 91, 7 Jan 92 to 11 Jan 92, 17 Feb 92 to 21 Feb 92[a], 21 Apr 92 to 24 Apr 92[a]. "a" indicates sampling during periods of biomass burning activity.

Sampling dates for the LCF site: 15 Apr 88 to 20 Jun 88, 15 Apr 89 to 23 Jul 89, 11 May 90 to 25 May 90, 30 Sep 91 to 29 Sep 92.

< 2 m s^{-1} are defined as "convective precipitation" (Table B-1). Events were separated using this criteria on the basis of meteorological data corroborated with visual observations. Most of the mist, advective precipitation and convective precipitation samples are "bulk" because collectors were exposed to dry deposition for up to 48 hours before the onset of an event.

Cloud Water

Cloud water was collected at the WCF site with Atmospheric Sciences Research Center (ASRC) passive cloud water collectors (Falconer and Falconer 1980). Collectors (30 cm tall, 10 cm diameter) consisted of acrylic plastic frames with ca. 100 Teflon monofilament lines (0.05 cm diameter) strung vertically between the top and base of the frames. Collectors were rinsed with an excess of deionized (DI-) water and then soaked in DI-water overnight before use. They were transported to the site in clean polyethylene bags and connected to polypropylene funnels (16 cm or 19.5 cm diameter) draining into polypropylene collection bottles. All funnels and bottles had been previously washed with 0.1 M HCl and rinsed 5-10 times with DI-water. Collectors, funnels and bottles were mounted on a PVC plastic frame 2.5 m above the floor of an observation deck. After cloud immersion occurred, polyethylene bags were removed from collectors and the first 10-20 ml of sample discarded. Sub-samples were transferred to polypropylene bottles washed in a similar manner as the collection bottles. Samples collected during intermittently dry (non-cloud) periods were discarded.

Mist and Advective Precipitation

Cloud water collectors were also used to collect mist and precipitation at both sites (Table B-1). At the LCF site, a cloud water collector was mounted at 17 m height on a meteorological tower and accessed with a rope and pulley system. Samples were collected no later than 72 hours after the onset of mist or precipitation. Subsamples were transferred to clean polyethylene bottles, and collectors were then either replaced with new, acid-washed and DI-water rinsed collectors or rinsed three times with an excess of DI-water and replaced.

Convective Precipitation

Convective precipitation was sampled at the LCF site only (Table B-1). A bulk precipitation-type collector was mounted 2 m above the forest floor in a large forest gap (1988,1989,1990) or from 17 m on a meteorological tower (1991-92). Samples were collected no later than 72 hours after the onset of precipitation. Subsamples were transferred to clean polyethylene bottles, and collectors were then either replaced with new acid-washed and DI-water rinsed collectors or rinsed three times with an excess of DI-water and replaced.

Meteorological Variables

A tipping bucket raingage (Model #2501, Sierra Misco Environmental Ltd., Victoria, B. C.) and an artificial foliar surface (30 cm tall, 1410 cm^2 foliar area) constructed of wire and plastic mounted above a second tipping bucket raingage mounted at 17m on a 27m meteorological tower were used to determine hourly precipitation depth and event duration at the LCF site in 1991-92. A 3-cup anemometer (Model #12-002, R. M. Young Co., Traverse City, Michigan) mounted at the top of the tower was used to measure windspeed. Instruments were recorded with an automated data logger (Easy Logger Model EL824-GP, Omnidata Inc., Ogden, Utah).

Chemical Analyses

Chemical analyses of cloud water and precipitation samples are described in Appendix A.

Data Analyses

Volume-weighted mean ion concentrations were calculated for cloud water, mist and advective precipitation samples collected within each event. Arithmetic means and standard deviations were then calculated for cloud water events, and volume-weighted mean ion concentrations were calculated for mist and advective precipitation events. Volume-weighted means were also calculated for convective precipitation samples. Correlation coefficients (Pearson's product-moment) were calculated for ion concentrations in cloud water, mist and both categories of precipitation. Wilcoxson Two-sample nonparametric tests (Sokol and Rohlf 1981) were used to detect differences in ion concentrations in cloud water among early dry season and late dry season sampling periods. Prior to statistical analyses, data were tested for normality and homoscedasticity of group variances. All statistical analyses were performed using SYSTAT statistical packages (Wilkinson 1987).

Results and Discussion

Cloud Water

Mean concentrations of H^+, NO_3^- and NH_4^+ in cloud water were 7 to 17 times greater than those in advective precipitation, and 10 to 45 times greater than those in convective precipitation (Tables B-2 and B-3). Concentrations of H^+, NO_3^-, and NH_4^+ in cloud water at Monteverde were 2-5 times greater than those in cloud water collected at Puerto Rico (Weathers et al. 1988)(Table B-4). Hydrogen ion concentrations were generally lower than those in cloud water at temperate montane sites, while NH_4^+ and NO_3^- concentrations were similar (Table B-4).

Sodium and Mg^{2+} concentrations were much greater in cloud water than those in both categories of precipitation. The molar ratio of Na^+ and Mg^{2+} in cloud water was similar

Table B-2. Means, standard deviations and ranges of ion concentrations in cloud water (n = 15 events).

Ion	Mean	s.d.	Range
	μmol l^{-1}		
H^+	132.1	149.8	2.5 to 489.8
$NO_3{}^-$	102.8	82.0	32.1 to 382.9
$NH_4{}^+$	148.9	199.7	47.2 to 739.4
Na^+	365.0	175.7	144.4 to 713.4
Mg^{2+}	63.4	30.9	18.1 to 121.8
Ca^{2+}	35.2	20.0	8.7 to 70.1
K^+	30.7	18.4	7.7 to 76.5

Table B-3. Volume-weighted mean ion concentrations (μmol l^{-1}) in mist (n=32), advective precipitation (n=54), and convective precipitation (n=47).

Precipitation Type	Ion Concentration (μmol l^{-1})		
	H^+	NO_3^-	NH_4^+
Mist	30.8 (0.2-251.2)	37.3 (10.8-106.1)	45.3 (2.8-131.1)
Advective Precipitation	19.0 (3.7-91.2)	7.5 (1.3-47.1)	8.9 (0.6-87.2)
Convective Precipitation	13.8 (2.8-55.0)	3.4 (bdl-46.8)	3.3 (bdl-127.8)

Ranges are in parentheses.
bdl = below detection limits.

Table B-3--continued

Precipitation Type	Ion Concentration (μmol l^{-1})			
	Na^+	Mg^{2+}	Ca^{2+}	K^+
Mist	183.0 (45.7-839.5)	21.9 (4.9-137.4)	16.8 (6.0-78.6)	13.5 (2.3-71.4)
Advective Precip.	75.4 (7.4-765.6)	8.8 (0.8-104.9)	6.6 (3.0-49.4)	4.1 (1.3-94.6)
Convective Precip.	7.8 (2.6-107.0)	1.2 (bdl-8.2)	3.4 (bdl-11.7)	2.1 (bdl-27.6)

Ranges are in parentheses.
bdl = below detectable limits.

Table B-4. Cloud water chemistry (mean μmol l^{-1}) at selected tropical and temperate montane sites.

Ion Concentration (μmol l^{-1})							Reference
H^+	NO_3^-	NH_4^+	Na^+	Mg^{2+}	Ca^{2+}	K^+	
Tropical Sites							
132	103	149	365	63	35	31	This study
20	60	32	650	85	63	25	Weathers et al. 1988[a]
Temperate U.S. Sites							
288	195	108	30	-	-	10	Lovett et al. 1982[b]
274	115	124	-	-	-	-	Mohnen and Kadlecek 1989[c]
205	155	84	13	2	5	3	Sigmon et al. 1989[d]
270	180	102	32	19	10	11	Schaefer and Reiners 1990[e]
335	130	175	-	-	-	-	Aneja et al. 1992[f]
122	62	74	3	3	11	3	Miller et al. 1993a[g]

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a. Pico del Oeste, Puerto Rico
b. Mt. Moosilauke, New Hampshire
c. Whiteface Mountain, New York, 5-year mean of summer values
d. Shaver Hollow, Virginia
e. Mt. Moosilauke, New Hampshire
f. Mt. Michell, North Carolina
g. Whiteface Mountain, New York; 4-year LWC weighted means

to that in sea water (0.137 ± 0.015 (mean ± 1 s.d) vs. 0.123), indicating that these ions originated primarily from wind-driven marine aerosol (Blanchard 1983). Marine-derived ions also accounted for a majority of the Na^+ and Mg^{2+} in cloud water collected at Puerto Rico (Weathers et al. 1988) (Table B-4). In contrast, Ca^{2+} and K^+ were relatively less enriched in cloud water when compared to mist and precipitation (Tables B-2, B-3).

With the exception of H^+ and other ions, all ion-pairs in cloud water were positively correlated (Pearson's product moment, $P < 0.05$ or 0.01)(Table B-5). Interestingly, there was little relationship between NO_3^- and H^+. The relatively high concentrations of NH_4^+ in cloud water suggest that H^+ was partially neutralized by NH_3. In addition, free acidity in cloud water and precipitation at remote tropical sites may be largely controlled by weak organic acids rather than by mineral acid concentrations (Galloway et al. 1982, Keene et al. 1983, Andreae et al. 1988b, Weathers et al. 1988, Talbot et al. 1990a, Sanhueza et al. 1992), but these were not measured. Precipitation acidity may also be locally controlled by vulcanism at remote sites (Kelmann et al. 1982, Veneklaas 1990).

Cloud water samples collected towards the end of the dry season (late February to early May) had greater concentrations of NO_3^-, NH_4^+, K^+, and Ca^{2+} than those collected at the end of the transition season and in the

Table B-5. Correlation matrices (Pearson's product-moment) for ion concentrations in cloud water (n=15), mist (n=32), advective precipitation (n=54) and convective precipitation (n=47).

Cloud Water

	H^+	NO_3^-	NH_4^+	Na^+	Mg^{2+}	Ca^{2+}	K^+
H^+	-						
NO_3^-	.139	-					
NH_4^+	.362	.982**	-				
Na^+	-.250	.664**	.607*	-			
Mg^{2+}	-.266	.626*	.574*	.987**	-		
Ca^{2+}	-.177	.786**	.739**	.582*	.568*	-	
K^+	-.038	.929**	.880**	.681**	.665**	.933**	-

Mist

	H^+	NO_3^-	NH_4^+	Na^+	Mg^{2+}	Ca^{2+}	K^+
H^+	-						
NO_3^-	-.151	-					
NH_4^+	.048	.583**	-				
Na^+	.022	.575**	.365	-			
Mg^{2+}	.041	.673**	.433*	.959**	-		
Ca^{2+}	-.301	.738**	.497**	.670**	.725**	-	
K^+	-.190	.723**	.528**	.695**	.737**	.983**	-

Significance levels: * = $P < 0.05$, ** = $P < 0.01$.

Table B-5--continued

Advective Precipitation

	H^+	NO_3^-	NH_4^+	Na^+	Mg^{2+}	Ca^{2+}	K^+
H^+	-						
NO_3^-	-.086	-					
NH_4^+	.102	.896**	-				
Na^+	-.019	.683**	.668**	-			
Mg^{2+}	-.067	.705**	.671**	.981**	-		
Ca^{2+}	-.063	.701**	.676**	.673**	.740**	-	
K^+	-.128	.845**	.713**	.847**	.862**	.793**	-

Convective Precipitation

	H^+	NO_3^-	NH_4^+	Na^+	Mg^{2+}	Ca^{2+}	K^+
H^+	-						
NO_3^-	.411**	-					
NH_4^+	.443**	.950**	-				
Na^+	.072	.441**	.574**	-			
Mg^{2+}	.099	.584**	.488**	.743**	-		
Ca^{2+}	.196	.570**	.527**	.759**	.636**	-	
K^+	.362*	.441**	.363**	.872**	.675**	.642**	-

Significance levels: * = $P < 0.05$, ** = $P < 0.01$.

early dry season (December and January) (Wilcoxon Two-sample tests, $P < 0.05$, Fig B-1). Differences in H^+, Na^+ and Mg^{2+} concentrations among these periods were not detected. Sampling periods towards the end of the dry season coincided with noticeable haze layers presumably due to burning of agricultural and forest biomass, and grey to black particulates were noted on cloud water collectors and in samples. It is likely that ion enrichment in cloud water samples collected towards the end of the dry season resulted from the incorporation of gases and particles derived from biomass burning activities (Andreae et al. 1988a, Crutzen and Andreae 1990, Lobert et al. 1990).

Mist and Advective Precipitation

In general, ion concentrations in mist and advective precipitation were inversely proportional to precipitation intensity; ion concentrations in mist were ca. 2 to 4 times greater than those in advective precipitation (Table B-3). Most ion-pairs in mist and advective precipitation were positively correlated, but again there was little relationship between H^+ and the other ions (Table B-5).

Convective Precipitation

Volume weighted mean ion concentrations in convective precipitation were generally lower than those in advective precipitation. Concentrations of H^+, Ca^{2+} and K^+ were relatively less reduced than those of the other ions,

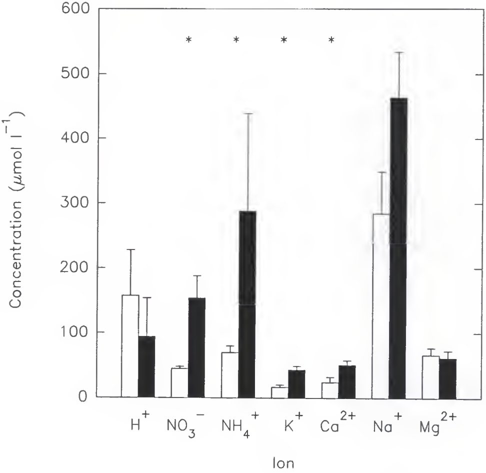

Figure B-1. Ion concentrations (μmol l^{-1}) in cloud water samples collected in the late transition to early dry season (open bars) and middle to late dry season (closed bars) (* = $P < 0.05$, Wilcoxson Two-sample Tests).

suggesting that sources of these ions exist through the wet season. Control of H^+ concentrations in convective precipitation by weak organic acids is probable and has been discussed previously. Calcium and K^+ in convective precipitation was possibly due to the release of coarse particles from the forest canopy, and/or from soil (Crozat 1979, Artaxo et al. 1990, Talbot et al. 1990b)(Table B-3). Most ion-pairs were positively correlated with the exception of H^+ and Na^+, Mg^{++} and Ca^{++} ion-pairs (Table B-5). In contrast to cloud water, mist and advective precipitation, NO_3^- and NH_4^+ were positively correlated with H^+ in convective precipitation. Concentrations of NO_3^-, NH_4^+, Ca^{2+} and K^+ in convective precipitation declined rapidly through the three wet seasons monitored, as previously reported for other tropical sites (Lewis 1981, Kellman et al. 1982, Hendry et al. 1984). Decreases in ion concentrations are presumably due to the washout of haze layers and reduced agricultural burning activity as the wet season progresses (Lewis 1981, Andreae et al. 1990, Crutzen and Andreae 1990).

Sources of Inorganic Nitrogen in Cloud Water and Precipitation

The relatively high concentrations of NO_3^- and NH_4^+ in cloud water and mist reported here suggest that emissions of NO_x, NH_3 and particles containing NO_3^- and NH_4^+ are considerable downwind from the sites throughout the dry season. Since no major urban areas or industrial sources of NO_x or NH_3 exist in the predominant wind direction, emissions likely originated primarily from forest and agricultural ecosystems. Other sources of NO include production during lightning discharges and downward transport of NO_x from the stratosphere (Logan 1983, Ayers and Gillet 1988). Long-distance transport may also be a minor source of NO_3^- in cloud water and precipitation at this site (Savoie et al. 1989, 1992).

Much of the NO_3^- and NH_4^+ in cloud water and precipitation originates from gas-phase precursors (NO_x and NH_3). Gas-phase reaction of NO_x and OH, which is produced rapidly during the daytime due to considerable photochemistry at tropical latitudes, leads to the production of HNO_3 (Crutzen 1987, Warneck 1988, Galbally and Gillet 1988). Heterogeneous-phase reactions of N_2O_5 and NO_3 on marine aerosol and cloud droplets may also lead to HNO_3 production at night (Dentener and Crutzen 1993). The roles of reactions involving N_2O_5 and NO_3 with dimethyl sulfide (DMS) from marine sources or hydrocarbons emitted from forest and agricultural ecosystems in the production of HNO_3 and particles containing NO_3^- are less clear. HNO_3 is highly reactive with particles and cloud droplets (Warneck 1988).

Oxidation of DMS and subsequent reaction with NH_3 is an important pathway for the production of cloud condensation nuclei in the remote marine atmosphere (Nguyen et al. 1983, Ayers and Gras 1991, Hegg et al. 1991, Quinn et al. 1993). Gas-to-particle conversion involving the reaction of NH_3

with H_2SO_4, HNO_3 or HCl, and heterogeneous-phase reactions on existing particles also lead to the formation of primarily submicron sized particles containing NH_4^+ (Quinn et al. 1987, Allen et al. 1988, Quinn et al. 1990). In addition, NH_3 is highly soluble in acidic cloud droplets (Quinn et al. 1987, Warneck 1988).

The burning of vegetation typically results in considerable loss of N and other ions from the site (Ewel et al. 1981, Crutzen and Andreae 1990, Kaufmann et al. 1993). Plant tissue N is volatilized as NO, NH_3, HCN, and other organic N compounds, and released as particulates containing N and other ions (Lobert et al. 1990, Kauffman et al. 1993). High concentrations of NO, HNO_3, PAN, and plant-derived organic particles containing NH_4^+, NO_3^-, K^+ and other ions have been associated with haze layers over the Amazon basin during the dry season (Crutzen et al. 1985, Delaney et al. 1985, Andreae et al. 1988, Artaxo et al. 1988, Talbot et al. 1988). Emissions of NO from soils may also be stimulated for some period following burning activities by undefined mechanisms (Anderson et al. 1988). Although there is a strong association between biomass burning and N-containing compounds in the atmosphere, regional emission inventories for the tropics are limited and subject to considerable uncertainties (Crutzen and Andreae 1990, Denmead 1990, Schlesinger and Hartley 1992). Therefore, it is currently difficult to accurately evaluate the contribution of biomass burning activities to inorganic N concentrations in cloud water and precipitation, or to N deposition to tropical ecosystems.

Recent evidence suggests that soils are also a major source of NO in tropical regions (Kaplan et al. 1988, Johansson et al. 1988, Bakwin et al. 1990, Sanhueza et al. 1990, Davidson et al. 1991, 1993). A number of lowland tropical soils are characterized by relatively rapid rates of N transformations, including nitrification (Vitousek and Sanford 1986, Vitousek and Matson 1988, Zou et al. 1992). Although few data exist linking rates of NO emission with nitrification rates, NO emissions are positively correlated with NH_4^+ levels in soil (Hutchinson et al. 1993), indicating that autotrophic nitrifying bacteria are important in the biogenic production of NO in relatively dry and coarse textured soils (Hutchinson and Brams 1992, Davidson et al. 1993, Hutchinson et al. 1993). In addition, inhibitors of nitrification reduced NO emissions to very low levels in laboratory experiments (Davidson et al. 1993, Hutchinson et al. 1993). Abiotic production of NO via chemodenitrification may result from the decomposition of HNO_2 in acidic soils or at acidic microsites in soil (Davidson et al. 1993).

A more complex situation exists in relatively wetter and perhaps in fine textured soils; at moderate soil moisture levels, gaseous diffusion of NO may be impeded by saturation of pore spaces while the activity of autotrophic nitrifiers is less affected, resulting in lower $NO:NO_3^-$

production ratios (Davidson et al. 1993). Further increases in soil moisture and the resultant low partial pressures of O_2 in soil ultimately limits the activity of nitrifying bacteria. Denitrification becomes an important pathway of both NO and N_2O production in relatively more saturated soils, but emission rates of NO are typically much lower than those from drier soils (Bakwin et al. 1990, Hutchinson et al. 1993). At the highest soil moisture levels, gaseous emissions of N are dominated by N_2 and to a lesser extent N_2O via denitrification (Paul and Clark 1989).

Current changes in land use are likely to increase emissions of NO because production and release from pastures and croplands may be greater than that from forest soils (Davidson et al. 1991, Hutchinson and Brams 1992, Williams et al. 1992, Keller et al. 1993). Relatively sparse canopies in agricultural ecosystems allow greater soil insolation, leading to higher soil temperatures which stimulates the activity of autotrophic nitrifiers and other organisms important in NO production (Hutchinson and Brams 1992). Nitrogen amendments, especially as NH_4^+ -N and NO_2^- -N, have stimulated NO emission from a variety of forest and agricultural soils (Bakwin et al. 1990, Davidson et al. 1991, Hutchinson and Bram 1992, Hutchinson et al. 1993, Davidson et al. 1993). In addition to lower rates of NO emission from forest soils, a greater proportion of the emitted NO may be subsequently deposited as HNO_3, NO_2, PAN, and other N species following oxidation on the aerodynamically rougher forest canopy (Bakwin et al. 1990, Jacob and Wofsey 1990, Lovett and Lindberg 1993).

With the exception of rice paddies (Vlek and Byrnes 1986), emission inventories for NH_3 are virtually non-existent in tropical regions (Galbally and Gillett 1988, Denmead 1990, Schlesinger and Hartley 1992). Volatilization from plant litter, animal waste, and agricultural soils are presumably the major sources of NH_3 other than biomass burning (Harper et al. 1983, Galbally and Gillet 1988, Pain et al. 1989, Whitehead and Lockyer 1989, Whitehead and Bristow 1990, Whitehead and Raistrick 1990, Sutton et al. 1993). Conversion of forest to pasture and cropland may also lead to increased emission of NH_3 in tropical regions. Ammonia emissions from acidic forest soils are probably minimal, while volatilization of NH_3 from cattle urine and manure in pastures may be considerable (Harper et al. 1983, Pain et al. 1989, Lockyer and Whitehead 1990). Volatilization of fertilizer N as NH_3 may also occur from croplands, but emission rates are strongly dependent upon fertilizer type, application technique, and meteorological conditions (Harper et al. 1983, Whitehead and Raistrick 1990).

Seasonal biomass burning is now ubiquitous in the tropics and clearly affects regional atmospheric and precipitation chemistry (Andreae et al. 1988a, 1990, Crutzen and Andreae 1990, Keller et al. 1991). The role of changes in land use in altering emissions of trace gasses is less well known, and requires a systematic inventory coupled with process-oriented investigations. Especially poor is our knowledge of the interactive effects of fertilizer type and application rates, cultural treatments, and soil moisture status on the relative rates of NO, N_2O, and N_2 emissions from tropical croplands and pasture (Davidson et al. 1991, Hutchinson and Bram 1992, Williamson et al. 1992, Keller et al. 1993). Although volatilization from livestock pastures is a major source of NH_3, we know less concerning rates of NH_3 emission from crop plants, plant litter and agricultural soils in the tropics. We also lack long-term emission data for all tropical ecosystems because previous measurements have been made on a short-term basis only.

Rates of forest clearing in Costa Rica have increased over the period from 1941 to 1983 (Sader and Joyce 1988), primarily for conversion to pasture and other agricultural uses (Veldkamp et al. 1992, Reiners et al. 1994). These activities have produced a regional mosaic of pasture, agricultural lands and managed forest. The potential for greater emissions of N containing compounds due to these changes in land use has considerable implications for the chemistry of cloud water and precipitation, and thus increased deposition of N to Monteverde and other TMCFs.

APPENDIX C
DEPOSITION AND NET RETENTION OF INORGANIC NITROGEN AND SODIUM BY THE CANOPY AT A TROPICAL MONTANE CLOUD FOREST SITE

Introduction

Deposition and canopy-atmosphere interactions of inorganic nitrogen (N) in temperate montane cloud forest ecosystems have received considerable attention in the last decade, in part because of the hypothesized roles of increased N deposition in forest decline, N saturation and acidification of soils, and increased levels of nitrate (NO_3^-) and acidity in surface waters (Nihlgard 1985, Aber et al. 1989, Schultze et al. 1989, Johnson and Lindberg 1992, Stevens et al. 1994). Inorganic N in cloud water often accounts for a significant portion of the total N deposition to montane cloud forests because (i) concentrations of nitrate (NO_3^-) and ammonium (NH_4^+) in cloud water are typically three to ten times greater than those in precipitation (Fowler et al. 1988, Weathers et al. 1988, Mohnen and Kadlecek 1989), (ii) montane areas are frequently immersed in cloud (Lovett and Kinsman 1990, Vong et al. 1991, Bruijnzeel and Proctor 1993), (iii) foliage, branches, and epiphytic vegetation are aerodynamically rough surfaces (Nadkarni 1984, Lovett and Reiners 1986, Monteith and Unsworth 1990), and (iv) canopy resistance to cloud water deposition via impaction is low when cloud immersion is coupled with the relatively high wind speeds characterizing many montane areas (Lovett 1984, Beswick et al. 1991, Gallager et al. 1992). As a result, total inorganic N deposition is typically greater to montane cloud forests when compared to lower elevation forests which receive only wet and dry deposition (Fowler et al. 1988, Crossley et al. 1992, Lovett and Lindberg 1993, Miller et al. 1993a).

Net retention of inorganic N by the canopy is typically estimated by comparing measured or modeled estimates of total inorganic N deposition to N fluxes in throughfall and stemflow (TF+ST). Numerous investigations in temperate forest ecosystems have indicated that the canopy retains inorganic N from atmospheric deposition, and that net retention rates are positively correlated with deposition rates (Parker 1983, Lovett and Lindberg 1993, Stevens et al. 1994, Van Ek and Draaijers 1994). Considerably fewer estimates exist for atmospheric deposition and net retention of inorganic N by the canopy in TMCF (Asbury et al. 1988, Veneklaas 1990, McDowell and Asbury 1993). However, seasonal biomass burning, conversion of forest to pasture and croplands, and other land use changes have increased N emissions in tropical regions (Galloway 1989, Crutzen and Andreae 1990, Keller et al. 1991, Galloway et al. 1994), resulting in concentrations of inorganic N in cloud water and precipitation that are similar to those at a number of N. American and European sites (Appendix B). The canopy of

TMCF is aerodynamically rough due to high leaf areas and abundant epiphytes, and may retain a major portion of the inorganic N deposited from the atmosphere (Clark and Nadkarni 1990, McDowell and Asbury 1993, Clark et al. 1993). Since many epiphytes are closely linked to atmospheric sources of N (Nadkarni 1984, Benzing 1990, Chapter 4), estimates of atmospheric deposition and net retention of inorganic N by the canopy are necessary to evaluate the potential effects of increased N deposition to the diverse canopy biota and TMCF ecosystems as a whole. The objectives of this study were to estimate: (i) atmospheric deposition of inorganic N to the canopy, and (ii) net retention of deposited inorganic N by the canopy at a TMCF site.

Methods and Materials

General Approach

Meteorological variables (precipitation depth, net cloud water and precipitation depth, windspeed, shortwave radiation, temperature, and relative humidity) were measured above the canopy from a 27 m meteorological tower located in a small gap at the field site. Bulk precipitation (BP) and bulk cloud water and precipitation (BCWP) samples were collected at 17 m on the tower. Throughfall (TF) was collected in 20 plots distributed at random locations over 1 ha of primary forest adjacent to the tower. Bulk precipitation, BCWP and TF were sampled continuously from 30 September 1991 to 29 September 1992. Total deposition (cloud + wet + dry) of inorganic N to the canopy was estimated using a sodium (Na^+) mass balance technique.

Meteorological Variables

Precipitation depth was measured with a tipping bucket raingage (Model #2501, Sierra-Misco Environmental Ltd. Victoria, B.C.) mounted at 12 m height on a boom extending 3 m out from the meteorological tower. Net cloud water and precipitation depth was measured with an artificial foliar surface (30 cm tall, 1410 cm^2 foliar area) constructed of wire and polypropylene "foliage" mounted above a funnel (30 cm diameter) connected to a second tipping bucket rain gage mounted at 17 m height on a boom extending 3 m out from the tower. Windspeed was measured with a 3-cup anemometer (Model #12-002, R. M. Young Co., Traverse City, Michigan) mounted at 27 m height on the top of the tower. Shortwave radiation was measured with a pyranometer (Model #LI-200S, Licor Inc., Lincoln, Nebraska) mounted at 27 m height on a boom extending 2 m out from the tower. Temperature and relative humidity were measured with a thermocouple and a resistance grid sensor (Model #PCRC-55, Phys-Chemical Research Corp., New York, New York) located in a small, well ventilated weather station (30 cm x 30 cm x 20 cm) mounted at 20 m height on the tower. All instruments were connected to an automated data logger (Easy Logger Field Unit model EL824-GP, Omidata International Inc., Logan, Utah). Precipitation and net cloud water and precipitation depths were recorded continuously to produce hourly sums. Windspeed, shortwave radiation, temperature and relative humidity were recorded for 10 seconds at 5 minute intervals and then integrated to produce hourly means.

Bulk Precipitation

Bulk precipitation was collected with a polypropylene funnel (16.3 cm diameter) attached to a 4 l polypropylene bottle. The mouth of the funnel was covered with polypropylene mesh (0.2 cm mesh size) to exclude litter and insects. The BP collector was supported in a PVC plastic frame and positioned at 17 m height on a boom extending 3 m out from the tower with a rope and pulley system. When BP was collected, volume was measured and samples were transferred to 125 ml polypropylene bottles which had been previously washed in 0.1 M HCl and rinsed at least 5 times with DI-water. The funnel and bottle were brushed out with a nylon brush and rinsed at least 3 times with DI-water, or replaced with new, clean funnels, mesh and bottles. The collector was then reassembled and repositioned on the tower.

Bulk Cloud Water and Precipitation

Bulk cloud water and precipitation was collected with an Atmospheric Sciences Research Center-type passive cloud water collector (Falconer and Falconer 1980). The collector (30 cm tall, 10 cm in diameter) consisted of an external ring of 100 Teflon monofilament lines (0.05 cm diameter) and an internal ring of 8 acrylic plastic rods (1.0 cm diameter) mounted above a polypropylene funnel (16.3 cm diameter) attached to a 4 l polypropylene bottle. The BCWP collector was supported in the PVC plastic frame adjacent to the BP collector. Funnels were positioned 30 cm apart with the BCWP collector located downwind from the BP collector in the predominant wind direction to minimize interference. Samples were collected at the same time as BP samples, and the BCWP collector was rinsed or replaced in a similar manner as the BP collector.

Throughfall

Throughfall (TF) was collected in 20 plots distributed at random locations over 1 ha of primary forest adjacent to the meteorological tower. Plots (25 m^2) were kept clear of all vegetation above 30 cm and < 5 cm stem diameter at the ground. Throughfall depths were measured with standard rain gages (5 cm diameter orifice, read to the nearest 0.05 cm) mounted at 1 m above the forest floor. Samples for TF chemistry were collected with polypropylene funnels (12.5 or 19.5 cm diameter) attached to 2 l polypropylene bottles located within 1 m of the rain gages. Funnel heights were 0.7 to 1 m above the forest floor, and funnel mouths were covered with polypropylene mesh (0.2 cm mesh size) to reduce contamination by litter and insects.

Throughfall samples were collected at the same time as BP and BCWP samples. Samples were transferred to 125 ml polypropylene bottles which had been previously washed in 0.1 M HCl and rinsed at least 5 times with DI-water. Collectors were emptied, brushed out with a nylon brush, rinsed 3 times with DI-water, and reassembled or replaced with new, clean funnels, mesh and bottles. Throughfall depths measured with standard rain gages were compared to TF volumes in polypropylene bottles for a sub-set of events to detect any bias of the sampling network.

Sample Handling and Analyses

All BP, BCWP and TF samples were collected a 1 to 3 day periods depending on meteorological conditions. Samples were collected within 72 hours of the onset of cloud immersion or precipitation. Samples were filtered with Gelman 0.45 μ GF/A filters using a polypropylene syringe within 6 hours of collection (>95% of all samples). Filtered samples were stored for no longer than 2 weeks at 4 °C before NO_3^- -N and NH_4^+ -N determinations (Appendix A). Samples were stored at 4 °C before Na^+ determinations (Appendix A).

Criteria for Classifying Events

Cloud water and precipitation events were defined by periods of at least 12 hours without precipitation or net cloud water as recorded by the tipping bucket rain gages

(Appendix B). Single tips (0.025 cm depth) that were recorded by only one of the collectors during apparently dry periods were discarded. Data from the tipping bucket rain gages were corroborated by visual observations for a large sub-set of events, and events were separated into 4 categories: (i) advective cloud water and mist events, (ii) advective precipitation events, (iii) convective precipitation events, and (iv) mixed events (Appendix B). Most advective and mixed events were single events (>90%). Some of the convective precipitation samples integrated 2 to 3 days of convective precipitation activity; ca. 41% of the convective precipitation samples represented single events.

Data Analyses

Bulk precipitation and BCWP depths were calculated by dividing volumes collected by funnel diameters and then summing the results within event categories. Convective precipitation depth was estimated using the BP collector because slightly lower volumes in BCWP indicated that raindrops bounced off the top of this collector during low wind conditions. Occasional data logger failure precluded an annual total from the tipping bucket rain gage, but BP depths corresponded closely to precipitation depths all events recorded. Depths collected with the artificial foliar surface tipping bucket gage were not used to calculate a total annual depth because of occasional data logger failure and because this collector showed a slight interception loss during many events.

Pearson's product-moment correlation coefficients were calculated for volume, NO_3^-, NH_4^+ and Na^+ pairs in BP for convective precipitation, and in BCWP for advective and mixed precipitation. Ion fluxes in BP and BCWP were calculated by multiplying depths collected by the appropriate ion concentrations, and then summing the products.

Throughfall depths were summed separately for each plot to estimate spatial variability over the 1 ha site. Precipitation interception by the canopy was estimated by subtracting mean TF depths from BP depths for convective events, and from BP and BCWP depths for advective and mixed events. Canopy water storage capacity was estimated using the zero-intercept value for the regression of mean TF depth on convective precipitation depth for single events which followed relatively long dry periods (>48 hours) (Leyton et al. 1967). Ion fluxes to each TF collector were calculated separately to estimate spatial variability over the 1 ha site; fluxes were calculated by multiplying depths collected by the appropriate ion concentrations and then summing the products.

Total deposition (cloud + wet + dry) of NO_3^- -N and NH_4^+ -N to the canopy was estimated using a mass balance technique assuming conservative behavior for Na^+ in TF (Ulrich 1983, Van Ek and Draaijers 1994, D. Schaefer, pers. comm.). Sodium flux is stemflow (ST) was assumed to be 5%

of that in TF, and this value was added to the mean Na^+ flux in TF. Specific mass balance calculation were: (i) Na^+ flux in BP was subtracted from Na^+ fluxes in BCWP and TF + ST, (ii) the residual mean Na^+ flux in TF + ST was divided by the residual Na^+ flux in BCWP to calculate a "scaling factor", (iii) NO_3^- -N and NH_4^+ -N deposition in BP was subtracted from that in BCWP, and (iv) the residual NO_3^- -N and NH_4^+ -N fluxes in BCWP were multiplied by the "scaling factor", and this value was added back to the NO_3^- -N and NH_4^+ -N fluxes in BP to estimate total inorganic N deposition to the canopy. All statistical analyses were performed using SYSTAT statistical packages (Wilkinson 1987).

Results

Bulk Precipitation

Bulk precipitation depth was 319.1 cm for the year (Table C-1). Advective and mixed precipitation totalled represented 56% of the annual BP depth. Volume weighted mean concentrations of NO_3^- -N, NH_4^+ -N and Na^+ were highest in cloud water and mist; NO_3^- -N and NH_4^+ -N concentrations were lowest in mixed precipitation, and Na^+ concentrations were lowest in convective precipitation (Table C-1). Relative proportions of NO_3^- -N and NH_4^+ -N were similar in all types of precipitation. Volume was negatively correlated with NO_3^- -N, NH_4^+ -N and Na^+ concentrations, Table C-1. Depth (cm), and volume weighted mean concentrations (mg N l^{-1}) and deposition (kg N ha^{-1} yr^{-1}) of NO_3^--N, NH_4^+-N and Na^+ by event category in bulk precipitation (BP) from 30 September 1991 to 29 September 1992.

Event Category	Depth (cm)	Volume Weighted Concentration (mg l^{-1})			Deposition (kg ha^{-1} yr^{-1})		
		NO_3^--N	NH_4^+-N	Na^+	NO_3^--N	NH_4^+-N	Na^+
CW and Mist (n=16)	5.7	0.35	0.33	4.25	0.2	0.2	2.4
Advective Precipitation (n=41)	134.2	0.06	0.05	0.96	0.8	0.8	12.9
Convective Precipitation (n=37)	139.9	0.04	0.04	0.19	0.6	0.6	2.6
Mixed Events (n=8)	39.2	0.02	0.03	0.41	0.1	0.1	1.6
Total for all Events (n=102)	319.1	0.05	0.05	0.61	1.7	1.7	19.5

Sample size is in parentheses.

while ion pairs were all positively correlated in convective precipitation (Table C-2). Deposition of inorganic N and Na^+ in BP was 3.4 kg N ha^{-1} yr^{-1} and 19.5 kg Na^+ ha^{-1} yr^{-1}, respectively (Table C-1). Bulk advective precipitation accounted for 59% of the inorganic N and 78% of the Na^+ deposition in BP.

Bulk Cloud Water and Precipitation

Bulk cloud water and precipitation depth was 407.4 cm for the year (Table C-3). Advective cloud water, precipitation and mixed precipitation depth totalled was 267.8 cm and represented 66% of the annual input in BCWP. Consistently greater depths were collected as BCWP when compared to BP during advective cloud water and precipitation events, indicating that the BCWP collector was more effective at capturing wind-driven droplets. Cloud water and precipitation depth in BCWP was 1.5 times greater than that in BP for all advective events totaled, and 2.2 times greater for cloud water and mist events.

Volume weighted mean concentrations of NO_3^- -N, NH_4^+ -N and Na^+ in BCWP were highest in cloud water and mist; NO_3^- -N and NH_4^+ -N concentrations were lowest in mixed precipitation, and Na^+ concentrations were lowest in convective precipitation (Table C-3). Concentrations of NO_3^- -N, NH_4^+ -N and Na^+ were consistently greater in BCWP when compared to those in BP within the same advective or mixed

Table C-2. Correlation coefficients (Pearson product-moment) for depth and concentrations of NO_3^-, NH_4^+ and Na^+ in (i) convective precipitation collected as BP, (ii) advective cloud water and precipitation collected as BCWP, and (iii) all precipitation categories.

Convective Precipitation (n=37)

	Depth	NO_3^-	NH_4^+	Na^+
Depth	-			
NO_3^-	-.363	-		
NH_4^+	-.260	.949**	-	
Na^+	-.404	.474*	.582**	-

Advective Cloud Water and Precipitation (n=57)

	Depth	NO_3^-	NH_4^+	Na^+
Depth	-			
NO_3^-	-.419**	-		
NH_4^+	-.428**	.844**	-	
Na^+	-.446**	.854**	.784**	-

All Precipitation Categories (n=102)

	Depth	NO_3^-	NH_4^+	Na^+
Depth	-			
NO_3^-	-.363**	-		
NH_4^+	-.362**	.811**	-	
Na^+	-.353**	.870**	.802**	-

Significance levels: * = $P < 0.05$, ** = $P < 0.01$

Table C-3. Depth (cm), and volume weighted mean concentrations (mg N l^{-1}) and deposition (kg N ha^{-1} yr^{-1}) of NO_3^- -N, NH_4^+ -N and Na^+ by event category in bulk cloud water and precipitation (BCWP) from 30 September 1991 to 29 September 1992.

Event Category	Depth (cm)	Volume Weighted Concentration (mg l^{-1})			Deposition (kg ha^{-1} yr^{-1})		
		NO_3^--N	NH_4^+-N	Na^+	NO_3^--N	NH_4^+-N	Na^+
CW and Mist (n=16)	12.5	0.56	0.56	7.34	0.7	0.7	9.2
Advective Precipitation (n=41)	215.8	0.10	0.11	1.64	2.2	2.3	34.4
Convective Precipitation (n=37)	139.9	0.04	0.04	0.19	0.6	0.6	2.6
Mixed Events (n=8)	39.5	0.06	0.05	0.51	0.2	0.2	1.6
Total for all Events (n=102)	407.7	0.09	0.09	1.18	3.7	3.8	48.2

Sample size is in parentheses.

precipitation event, suggesting that ion concentrations were relatively greater in smaller, wind-driven droplets, although dry deposition of these ions to the BCWP collector may also have been greater. Volume was negatively correlated with NO_3^- -N, NH_4^+ -N, and Na^+ concentrations, while ion pairs were all significantly correlated for advective cloud water and precipitation (Table C-2).

Deposition of inorganic N and Na^+ in BCWP was 7.5 kg N ha^{-1} yr^{-1} and 48.2 kg Na^+ ha^{-1} yr^{-1}, respectively (Table C-3). Bulk advective cloud water and precipitation accounted for 79% of the total inorganic N deposition and 90% of total Na^+ deposition in BCWP. Inorganic N deposition in BCWP was 2.8 times greater than that in BP for all advective events, and 3.5 times greater for cloud water and mist events.

Throughfall

Throughfall depth was 206.7 ± 13.0 cm (mean ± 1 s.e., n=20) for the year (Table C-4). Interception was estimated at 29% of incident precipitation during convective precipitation events, and 35% of BP and 49% of BCWP for all events. Canopy water storage was estimated at ca. 3.5 cm for eight convective precipitation events which were intercepted by an initially dry canopy (Figure C-1).

Volume weighted mean concentrations of NO_3^- -N, NH_4^+ -N and Na^+ in TF were greatest for cloud water and mist events (Table C-4). Nitrate -N concentrations were much lower

Table C-4. Depth (mean cm ± 1 s.e., n=20) and volume weighted mean concentrations of NO_3^- -N, NH_4^+ -N and Na^+ in throughfall by event category for 30 September 1991 to 29 September 1992.

Event Category	Depth (cm)	Volume Weighted Mean Concentrations (mg l^{-1})		
		NO_3^- -N	NH_4^+ -N	Na^+
CW and Mist (n=16)	1.9 ± 0.3	0.07	0.21	6.86
Advective Precipitation (n=41)	76.0 ± 7.1	0.02	0.07	2.87
Convective Precipitation (n=37)	99.3 ± 5.8	0.04	0.06	1.30
Mixed Events (n=8)	29.2 ± 2.0	0.03	0.04	1.62
Total for all Events (n=102)	206.7 ± 13.0	0.03	0.06	1.97

Sample size is in parentheses.

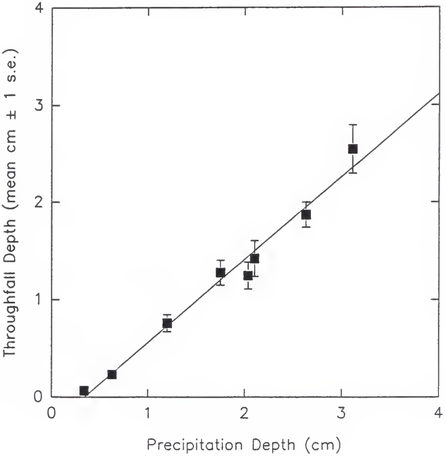

Figure C-1. Plot of precipitation depth (cm) vs. throughfall depth (mean cm ± 1 s.e.) for 8 convective precipitation events intercepted by an initially dry canopy.

while NH_4^+ -N concentrations were moderately lower when compared to those in advective cloud water and precipitation collected as BCWP, indicating preferential net retention of NO_3^- -N by the canopy. Nitrate -N concentrations were similar and NH_4^+ -N concentrations were slightly enriched when compared to those in convective and mixed precipitation. Inorganic N flux to the forest floor was 1.9 ± 0.3 kg N ha^{-1} yr^{-1} (mean ± 1 s.e.)(Table C-5). Nitrate -N accounted for only 25% of the inorganic N flux to the forest floor during advective events, and 39% during convective and mixed precipitation events.

Deposition and Net Retention of Inorganic Nitrogen by the Canopy

Total deposition (cloud + wet + dry) of inorganic N to the canopy was estimated at 6.7 kg N ha yr^{-1}, representing ca. 0.89 times the input to the BCWP collector. Net retention of NO_3^- -N and NH_4^+ -N by the canopy represented 81% and 61% of total deposition, respectively (Table C-6). Net retention of NO_3^- -N represented 91% of deposition for all advective cloud water and precipitation events, and 38% of deposition for convective precipitation events. Net retention of NH_4^+ -N represented 73% of deposition for all advective cloud water and precipitation events, and only 5% of deposition for convective precipitation events (Table C-6).

Table C-5. Mean NO_3^- -N, NH_4^+ -N and Na^+ fluxes (mean kg ha^{-1} yr^{-1} ± 1 s.e., n=20) in throughfall by event category for 30 September 1991 to 29 September 1992.

Event Category	Throughfall Flux (mean kg ha^{-1} yr^{-1} ± 1 s.e.)		
	NO_3^- -N	NH_4^+ -N	Na^+
CW and Mist (n=16)	0.01 ± 0.00	0.03 ± 0.01	1.29 ± 0.32
Advective Precipitation (n=41)	0.17 ± 0.04	0.53 ± 0.05	21.85 ± 2.88
Convective Precipitation (n=37)	0.37 ± 0.14	0.58 ± 0.09	13.39 ± 1.74
Mixed Events (n=8)	0.05 ± 0.02	0.09 ± 0.02	4.75 ± 0.75
Total for All Events (n=102)	0.62 ± 0.21	1.31 ± 0.13	41.28 ± 5.12

Sample size is in parentheses.

Table C-6. Deposition of NO_3^- -N and NH_4^+ -N to the canopy estimated using a Na^+ mass balance, mean NO_3^- -N and NH_4^+ -N fluxes in throughfall (from Table C-5) and percent net retention of NO_3^- -N and NH_4^+ -N by the canopy by event category.

Event Category	Deposition to Canopy (kg ha^{-1} yr^{-1})		Throughfall Flux (kg ha^{-1} yr^{-1})		Percent Net N Retention (%)	
	NO_3^--N	NH_4^+-N	NO_3^--N	NH_4^+-N	NO_3^--N	NH_4^+-N
CW and Mist	0.6	0.6	0.01	0.04	98	93
Advective Precipitation	1.9	2.0	0.17	0.53	91	74
Convective Precipitation	0.6	0.6	0.37	0.57	38	5
Mixed Precipitation	0.2	0.2	0.08	0.16	60	20
All Events	3.3	3.4	0.62	1.31	81	61

Discussion

Hydrologic Input

The proportion of advective cloud water and precipitation inputs calculated by subtracting BP from BCWP depths were within the range of proportions of horizontal precipitation inputs (c.f. Stadtmuller 1987, Bruijnzeel and Proctor 1993) reported from other tropical montane cloud forests where similarly designed collectors were used (Table C-7). Absolute depths of advective cloud water and precipitation were greater at this site (Table C-7).

While advective cloud water and precipitation inputs are typically estimated with artificial surfaces, considerable uncertainties exist in using these estimates to calculate deposition directly to an aerodynamically rough forest canopy (Lovett 1988, Cavelier and Goldstein 1989, Brunzjeel and Proctor 1993). Other methods to estimate hydrologic inputs in advective cloud water and precipitation to forest canopies include the hydrologic balance technique (Lovett 1988) and modelling cloud water deposition (Lovett 1984, Beswick et al. 1991, Gallager et al. 1992, Miller et al. 1993b). Both of these methods have limitations and typically require extensive hydrological and meteorological measurements. For example, an assumption implicit in the hydrologic balance method is that canopy surfaces are completely saturated or that the amount of water stored by the canopy is in steady state; for a canopy with abundant

Table C-7. Incident precipitation (cm yr^{-1}) collected with rain gages, additional cloud water and precipitation inputs (cm yr^{-1}) collected with ASRC or Nagel-type collectors, and advective cloud water and precipitation as a percentage of incident precipitation at TMCF sites.

Location	Incident Precipitation (cm yr^{-1})	Cloud Water and Precipitation (cm yr^{-1})	Percent Cloud Water and Precipitation (%)
Monteverde, Costa Rica[a]	319.1	88.6	28
Pu'u La'au, Hawaii[b]	25.7	9.8	38
Jalapa, Mexico[c]	59.7	12.5	21
Altotonga, Mexico[c]	74.6	16.6	22
Macuira, Colombia[d]	85.3	79.3	93
Teziutlan, Mexico[c]	94.2	15.9	17
Tortutla, Mexico[c]	108.2	33.9	31
Santa Ana, Venezuela[d]	163.0	52.2	32
Cerro Copey, Venezuela[d]	446.1	49.1	11

a. This study
b. Juvik and Nullet 1993
c. Vogelmann 1973
d. Cavelier and Goldstein 1989

epiphytes and thus a large water storage capacity, this assumption may result in considerable error in the estimation of hydrologic inputs to the canopy. In addition, the hydrologic balance method relies on accurate TF+ST estimates which may be difficult to obtain in these structurally complex forest (Lovett 1988, Lloyd and Marques 1988, Puckett 1991).

Modelling approaches to estimate cloud water deposition to forest canopies have been successful at a number of temperate cloud forest sites (Lovett 1984, Beswick al. 1991, Miller et al. 1993a), but most cloud water deposition models rely on accurate estimates of the liquid water content of cloud which requires relatively complex meteorological instrumentation. In addition, these multiple resistance models were designed to simulate cloud water deposition only, and have not been used successfully to estimate the deposition of advective mist and precipitation to a forest canopy. Advective precipitation may be the major hydrologic inputs to many tropical montane forests (Tables C-2 and C-4; G. Lovett pers com.), and accurate estimation of these inputs represents an important challenge for future research.

Cloud Water and Precipitation Interception

Precipitation interception by the canopy calculated for convective precipitation events at this site was within the range of interception estimates from other tropical lower montane and montane cloud forests, while cloud water and precipitation interception for all events calculated from BP and BCWP depths exceeded this range (Figure C-2). Factors which may have contributed to the relatively high rates of precipitation interception at this site include: (i) rates of evaporation from forests on leeward slopes may be relatively large when compared to those from windward and ridge top forests, (ii) advection of energy from the surrounding lowlands may be a significant portion of the energy budget, (iii) hydrologic flux to stems may have been relatively large, and (iv) TF sampling was biased and underestimated hydrologic flux to the forest floor.

Since the site is located to the lee of the continental divide and was often at or below the trailing edge of the hill cap cloud, shortwave radiation flux and vapor pressure deficit of the atmosphere may have been greater at this site than those characterizing other TMCF sites. Frequent but intermittent cloud water and precipitation inputs to the canopy, coupled with it's relatively large water storage capacity (calculated at ca. 1.0 cm; Chapter 5) and relatively low resistances to water vapor loss may have resulted high rates of evaporation from the canopy (Gallager and Choularton 1989). Transpiration from abundant vascular epiphytes and hemiepiphytes, many of which have access to water stored in the large accumulations of DOM, may also have contributed to high rates of evaporation and hence precipitation interception at this site.

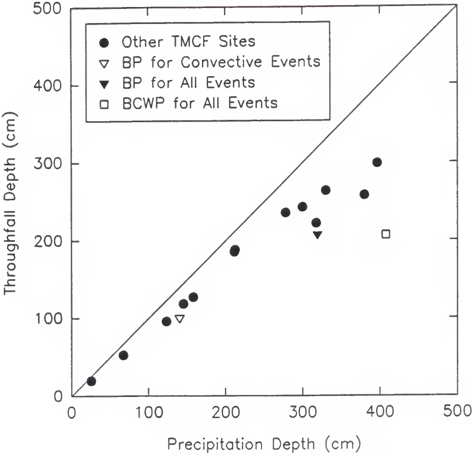

Figure C-2. Plot of precipitation depth (cm) vs. mean throughfall depth (cm) for tropical montane forest sites. Data from elfin forest sites are excluded.

A second, related phenomenon which may have resulted in relatively high rates of evaporation from the canopy at this site is the advection of energy from the surrounding lowlands (Calder 1990). The movement of relatively warm, dry air masses over the site was detected occasionally and may represent a significant portion of the energy budget, but the contribution of this additional energy to latent heat flux at this site is difficult to estimate.

Relatively high rates of precipitation interception may been confounded by the diversion of solutions via conduction through continuous mats of epiphytes to stems. Since stems have a high water storage capacity, solution storage may be considerable before stemflow is generated on the forest floor. Once stems are saturated, stemflow may represent a significant flux of water to the forest floor. It is notable that a number of tropical montane sites which received over 300 cm of precipitation had relatively high values for precipitation interception, suggesting that hydrologic flux to stems may be relatively large when continuous mats of epiphytes are saturated for long periods of time. Relatively large stemflow fluxes have been reported from elfin forest sites with a high density of stems (Weaver 1972), but information for other tropical montane forest sites is limited.

Lloyd and Marques (1988), Bruijnzeel (1990) and Puckett (1991) have noted that throughfall fluxes to the forest floor are highly variable in structurally complex forests, thus they are relatively difficult to sample accurately. However, when 26 to 40 throughfall collectors were used to sample TF at this site in 1988 (K. Clark, unpub. data), interception loss represented 32% of incident precipitation, similar to the results obtained in the 1991-92 sampling period reported here.

Inorganic Nitrogen and Sodium Deposition

Estimated NO_3^- -N, NH_4^+ -N and Na^+ deposition in BP at this site were within the range of estimates reported from other pre-montane and montane sites in the tropics (Table C-8). Deposition in BCWP at this site exceeded BP inputs reported from most sites with the exception of NO_3^- -N inputs reported from Venezuela, and NH_4^+ -N inputs reported from Colombia (Steinhardt and Fassbender 1979, Veneklaas 1990).

Estimated inorganic N deposition to the canopy calculated using the Na^+ mass balance resulted in greater inputs than those collected in BP and slightly lower inputs than those collected in BCWP. The N^+ mass balance technique represents a valuable method for estimating total deposition to tradewind-dominated sites because: (i) rates of Na^+ deposition are relatively high (Table C-8), (ii) Na^+, NO_3^- and NH_4^+ concentrations in cloud water and precipitation are significantly correlated, and (iii) precipitation interception is a relatively large portion of the latent heat flux, consequently rates of transpiration and Na^+ uptake

Table C-8. NO_3^- -N, NH_4^+ -N and Na^+ deposition (kg ha^{-1} yr^{-1}) in bulk precipitation at tropical pre-montane and montane sites.

Location	Deposition (kg ha^{-1} yr^{-1})		
	NO_3^- -N	NH_4^+ -N	Na^+
Monteverde, Costa Rica[a]			
1. BP	1.6	1.6	19.5
2. BCWP	3.7	3.8	48.2
Siguartepeque, Honduras[b]	0.3	n.d.	4.4
Turrialba, Costa Rica[c]	0.5	1.2	5.5
El Verde, Puerto Rico[d]	2.0	1.5	55.4
San Eusebio Venezuela[e]	9.9	n.d.	3.3
Santa Rosa de Cabal, Colombia[f]	n.d.	11.2	15.9
	n.d.	18.3	24.1
Blue Mnts. Jamaica[g]	n.d.	n.d.	20.3

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a. 28 September 1991 to 27 September 1992
b. Kellman et al. 1982
c. Hendry et al. 1984
d. McDowell et al. 1990; NO_3^--N and NH_4^+-N for wet-only deposition.
e. Steinhardt and Fassbender 1979
f. Veneklaas 1990; sites at 3370 m and 2550 m elevation.
g. Tanner 1977
n.d. = not determined.

from soil solutions may be relatively low (Grubb 1977, Bruijnzeel and Proctor 1993).

Estimated inorganic N deposition to the canopy at Monteverde was at the low end of the range of deposition estimates of 4.8 to 27 kg N ha yr^{-1} reported from 12 north temperate sites in the Integrated Forest Study (IFS; Lovett and Lindberg 1993). This reflects the facts that: (i) inorganic N in cloud water and precipitation at Monteverde primarily originates from natural and agricultural sources because no major urban areas or point sources of NO_x or NH_3 exist in the vicinity (Appendix B), (ii) cloud immersion was estimated to occur only ca. 7% of the time at this site, and (iii) dry deposition of HNO_3 and NH_3 were likely underestimated at this site. Although relatively long dry periods occurred infrequently, they were concentrated towards the end of the dry season when regional biomass burning activities were greatest. Since NO_3^- and NH_4^+ concentrations were highest in cloud water and precipitation during this period (Appendix B), it follows that atmospheric concentrations of HNO_3, NH_3 and other gasses and particles containing inorganic N were also relatively high during the end of the dry season.

Net Retention of Inorganic Nitrogen by the Canopy

Net retention of inorganic N by the canopy at Monteverde was within the range of 1 to 12 kg N ha yr^{-1}

reported from the 12 sites in the IFS (Lovett and Lindberg 1993). Percent net canopy retention of inorganic N was greater at Monteverde when compared to most IFS sites (71% vs. 50% ± 20% (mean ± 1 s.d.), range of 11% to 82%), but was closer to the values reported from the four sites where canopies had a substantial coverage of non-vascular epiphytes (62% ± 14% (mean ± 1 s.d.); Great Smokey Mountains, TN; Whiteface Mountain, NY; and two sites in Thompson Forest, WA)(Friedland et al. 1991, Johnson et al. 1991, Lovett and Lindberg 1993).

Net canopy retention of NO_3^- -N was greater than that for NH_4^+ -N at this site (81% vs. 61%), and NO_3^- -N flux in TF was only 47% that of NH_4^+ -N. The lower net retention rate of NH_4^+ -N may be partially due to leaching of DOM in the canopy (Vance and Nadkarni 1990, Coxson 1991, Chapter 6). Net retention of NO_3^- -N was approximately equal to that for NH_4^+ -N at the IFS sites, but NO_3^- -N fluxes in TF and ST were 1.5 to 6 times greater than that for NH_4^+ -N, reflecting relatively large dry deposition rates of HNO_3 and particles containing NO_3^- to a number of temperate forests. Net canopy retention of NO_3^- -N averaged 57% of inorganic N deposition for the four canopies in the IFS which had a substantial coverage of epiphytic vegetation (Lovett and Lindberg 1993).

Although biomass burning and other land use activities may have increased inorganic N concentrations in cloud water and precipitation, total inorganic N deposition was relatively low when compared to deposition estimates at a number of north temperate sites. The epiphyte-laden canopy at this site exerted a major effect on hydrologic and inorganic N inputs from the atmosphere: interception was relatively large and the canopy retained a majority of the inorganic N in atmospheric deposition, particularly of NO_3^- -N. Results from a canopy hydrology and N flux model suggested that epiphytic bryophytes and assemblages of epiphytic bryophytes, vascular epiphytes and DOM retained ca. 80% of the inorganic N retained by the canopy (Chapter 5). Because canopy components may retain inorganic N as a function of N additions from the atmosphere, the effects of increased, long-term N deposition to TMCF are unknown and await further investigation.

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BIOGRAPHICAL SKETCH

Kenneth Lawrence Clark was born to Paul and Carol Clark on October 27, 1958, in Englewood, New Jersey. He graduated from Point Loma High School in San Diego, California, in 1976, and then moved to Arcata, California, to attend Humboldt State University. He graduated with honors with a B. A. degree in botany in 1981 and an M. A. degree in biology in 1985.

He and his wife, Nancy Barbour, traveled throughout the Asian tropics before returning home to study and work at the University of Santa Barbara, California, Monteverde, Costa Rica, and later at the Marie Selby Botanical Gardens, Sarasota, Florida. He enrolled at the University of Florida in January, 1990. He is a tree climber, a surfer and a slide guitar player and has generally lived his life in the clouds.

I certify that I have read this study and that in my. opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the School of Forest Resources and Conservation in the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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